COMPARATIVE ECOLOGY AND BEHAVIOUR OF *CHAMAELEO PUMILUS PUMILUS* (GMELIN) AND *C. NAMAQUENSIS* A. SMITH (SAURIA: CHAMAELEONIDAE)

By
BRYAN RONALD BURRAGE
*South African Museum, Cape Town**

(With 14 figures and 49 tables)

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* Present address: College of the Desert, Palm Desert, California.

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I. INTRODUCTION

This study describes certain aspects of the life history of *Chamaeleo pumilus* (Gmelin) and of *C. namaquensis* A. Smith. Reproductive potential, population size, territorial structure, thermoregulation, behaviour, and other ecological relationships of these chamaeleonids in dynamic equilibrium with their vastly different habitats are considered. The viviparous, arboreal *C. pumilus* lives mostly in mesic areas of southern Africa. The aforementioned ecological considerations of the oviparous *C. namaquensis* have never been studied. This ground-dwelling species inhabits semi-arid and arid areas of southern Africa.

There is no comprehensive picture of chamaeleon ecology. Brain (1961) has given a preliminary picture of the life history and biology of *Chamaeleo dilepis*. Rose (1950) has made general comments on chamaeleons. Ecological studies on field populations of chamaeleons are so few and mostly of such limited scope as to be virtually non-existent. Following his papers on yearly population density variation of *C. pardalis* (Bourgat 1968*a*), and the spermatogenesis cycle of this insular species (Bourgat 1968*b*), Bourgat (1970) has provided a detailed study of *C. pardalis*. These are the only ecological studies on marked field populations of chamaeleons. Bourgat's papers and those of Saint Girons (1962) on sperm storage in female *C. basiliscus*, *C. chamaeleon*, and *C. lateralis*, Wager (1958), Bons & Bons (1960) on reproduction of *C. dilepis* and *C. chamaeleon*, respectively, are the only detailed field studies on chamaeleon reproduction, save short notes by Trench (1912) on *C. calcaratus* (=*C. chamaeleon zeylanicus*) and Menzies (1958) on *C. gracilis*. Chamaeleon colour lability has been the subject of very few serious studies. Until recently the general interpretation of this phenomenon has not altered much from those stated by Aristotle (Crosswell's translation, 1883) and Pliny (Bostock & Riley's translation, 1887). The function of chamaeleon colour lability has been discussed and investigated by Brücke (1852), Weber (1881), Fuchs (1914) and Krüger & Kern (1924). The dynamics of chamaeleon physiological thermoregulation were indicated in studies on the lungs and air sacs by Couvreur & Gautier (1904) and Tornier (1904), and the chamaeleonid carotid body (Adams 1957). Hogben & Mirvish (1928*a*, *b*) and Zoond & Eyre (1934) investigated colour change in *Chamaeleo pumilus* and *Lophosaura pumila* (both =*C. pumilus*) respectively, and Farghaly (1941) in *Chamaeleo vulgaris* (=*C. chamaeleon*), but few speculated on, or endeavoured to study its functional significance. Some of these early findings of the mediating mechanism of chamaeleon colour lability have been subsequently challenged and enlarged upon by Canella (1963) and Cleworth (unpublished data). There are no field records of chamaeleon body temperatures, but Stebbins (1961) gives body temperature records of captive *C. dilepis* and *C. namaquensis*. Parasites and disease of Madagascan chamaeleons have been studied by Brygoo (1963), Brygoo, Dodin & Sureau (1959) and Chabaud & Brygoo (1960). A fungal infection disturbing the colour lability mechanism is reported by Elkan (1965) for the East African *C. bitaeniatus*.

There are a number of papers based on captive chamaeleons, such as those by Abel (1931), Angel (1933), Atsatt (1953), Busack & Busack (1967), Bustard (1955, 1958, 1963, 1965, 1966, 1967*a*), and Von Frisch (1962), which are mostly short and often report results differing from findings on field studies of chamaeleons; a fact which only Bustard (1963) recognized might be true. A detailed discussion of the literature is given in the relevant sections of this paper to which they pertain.

A. *Systematics*

Knowledge of the life history and habits of our commonest reptiles, particularly lizards, is meagre. To avoid confusion as to the life history of which species or subspecies was examined, such studies should follow taxonomic investigations. Nevertheless, in many instances life history studies may help clarify systematics by providing clues to relationships, differences and similarities between closely related taxa. Studies in different areas of a widely distributed species' range help to assess its adaptations to diverse habitats and to determine the validity of recognized subspecies and perhaps the need for establishing others.

The Family Chamaeleonidae (or Chamaeleontidae) forms the Infraorder Rhiptoglossa, which, with the Infraorders Gekkota and Iguania (iguanids and agamids), comprises the Suborder Ascalabota. The Suborder Ascalabota is distinguished from the Suborder Autarchoglossa by the simple body musculature, tongue, and hemipenal structure and generally primitive character of the squamation (Camp 1923). Among the Ascalabota the superior temporal arch of Iguania distinguishes them from Gekkota. The acrodont dentition of chamaeleonids and agamids is sufficient to set them apart from iguanids which have pleurodont teeth.

Many Rhiptoglossa characters are shared with arboreal Gekkota (as partial zygodactyly in *Phyllurus;* reduction of body musculature and hoop-like parasterna in *Uroplates*) and arboreal Iguania (variously independent eye mobility, diverticulate lungs, prehensile tail, anterior pineal foramen, casque development and colour lability in *Agama*, *Anolis*, *Calotes*, *Chamaeleolis*, *Cophotis*, *Polychurus* and *Xiphocercus*). The Cuban iguanid *Chamaeleolis chamaeleontides* is most chamaeleonid-like, with which it shares partly fused eyelids, cranial casque development, and sluggish, deliberate movements (Wilson 1957). Only the Iguania and Rhiptoglossa have developed high laterally compressed arboreal forms. The only really distinctive Rhiptoglossa characters are the highly specialized feet and vermiform, highly extensile tongue, which, in Boulenger's (1885–87) and Gadow's (1901) view, justify their consideration as a separate infraorder; a view rejected by Romer (1956), Terentiev (1961), Mertens (1966) and others, as so many characters on which the separation is based are shared with others of the Infraorder Iguania in which these workers place the chamaeleonids. Cope (1864) was the first to regard the Rhiptoglossa as related to the Agamidae.

Saurians date back to the Upper Triassic; Upper Cretaceous lizards were essentially modern (Carroll 1969). The fossil record yields no undoubted chamaeleons, and those so assigned are based on jaw fragments with acrodont teeth that could equally be assigned to the agamids, from which the chamaeleonids could be derived (Camp 1923; Romer 1956). Leidy's (1873) *Chamaeleo pristinus* from the Eocene of Wyoming is most similar to the agamid *Calotes*, and thus not a chamaeleon. Camp (1923), Brock (1940), Malan (1946) and others consider chamaeleons as primitive survivors of some ancient pro-agamid-iguanid stock. Hillenius (1963, 1964) feels chamaeleons are of more recent origin, as the most primitive forms (*Chamaeleo chamaeleon* and allies) not only possess the characters one would expect in the hypothetical, ancestral chamaeleon, but also occupy the periphery of the chamaeleonid range (cf. Matthew 1915; Mayr 1954, 1963; Tihen 1949). Shute & Bellairs (1953), Hamilton (1960) and Schmidt (1964) have examined the inner ear structure of lizards to provide clues to their relationships. The latter two consider the chamaeleonid ear primitive—agreeing with Camp, Brock, Malan and others as to chamaeleonid affinities—whereas Miller (1966) thinks the chamaeleonid ear regressed or degenerate and distinct, neither supporting nor rejecting derivation of this group from the agamids, though the chamaeleon cochlear duct could conceivably derive from regression of the agamid type. Thus, most modern evidence indicates the distinctiveness of chamaeleonids, with possible close relationship to the agamids, but rejects the hypothesis that chamaeleons are survivors of an ancient pro-agamid-iguanid stock. This unsolved problem of chamaeleonid origin and affinities is not of further concern. Chamaeleon taxonomy is summarized below.

Terentiev (1961) recognizes 73 species of *Chamaeleon* (=*Chamaeleo*), Mertens (1966) 113 species of *Chamaeleo*, including *Microsaura*. *Chamaeleo* has the tail at least as long as the body, and smooth-scaled soles. *Chamaeleo namaquensis* is a possible exception with its lamellate soles, partly fringed toes, and tail much shorter or equal to body length. Mertens (1966) includes the five species of *Rhampholeon* with the seven species of *Brookesia* (=*Evoluticauda* and *Leandria*, Schmidt & Inger 1965). *Brookesia* and *Rhampholeon* have the tail shorter than the body, and spinose-scaled soles, but *Rhampholeon* differs by having bicuspid claws. *Chamaeleo* embraces the entire range of the Chamaeleonidae and is found in Africa, Madagascar, India, Ceylon, southern Spain, Asia Minor and Arabia; most are arboreal and oviparous. The exceptions are *Chamaeleo chamaeleon* and *C. namaquensis* which are cursorial, even fossorial in desert regions, and the *C. pumilus* and *C. bitaeniatus* groups which are viviparous. *Brookesia, sensu stricto,* is confined to Madagascar and is ground-dwelling on fallen leaves in forests. *Rhampholeon* (if a valid genus) is confined to tropical African rain forests in shrubs and undergrowth. The adaptations of chamaeleons show rigid specializations to an arboreal habitat, though some, as *Brookesia, sensu stricto*, *Chamaeleo chamaeleon*, and *C. namaquensis* have secondarily reverted to the ground. Chamaeleonids occur from sea-level to the Ethiopian Highlands and Ruwenzori Mountains, inhabiting the littoral to at least the mean high tide limit (conflicts with Neill 1958), forests, grassland, semi-arid scrub and deserts. Most species average 180 to 350 mm when fully matured (males usually smaller), with extremes of two Madagascan species: *Chamaeleo oustaleti* of nearly a metre, and *Brookesia minima* at 33 mm.

Chamaeleon taxonomy is confusing and best described as in a state of flux. Apart from whether chamaeleonids should be lumped with iguanids and agamids in the Infraorder Iguania or recognized as the separate Infraorder Rhiptoglossa, the family name has been changed several times, principally from Chamaeleonidae to Chamaeleontidae and vice versa, though there has been a myriad of other names and various taxonomic changes.

Gmelin (1789) originally described the Cape dwarf chamaeleon as *Lacerta pumila*, but Daudin (1802) renamed it *Chamaeleo pumilus*, when referring it to the Chamaeleonidae. Gray (1864) recognized Chamaeleonidae as the family name. In the same paper he renamed *Chamaeleo pumilus*, *Lophosaura pumila*. However, *Lophosaura* was preoccupied by a group of South American lizards Gray himself had previously described. Thoughtfully, Gray put the viviparous *melanocephala* (now considered at most a subspecies of *Chamaeleo pumilus*) into the genus *Microsaura*. *Lophosaura* was recognized as valid in subsequent taxonomic revisions, such as those of Methuen & Hewitt (1913), Hewitt (1935) and Power (1932), but since a preoccupied name cannot stand and since *Microsaura melanocephala* was later included in the *pumila* group, the name *Microsaura* took precedence (FitzSimons 1943). Werner (1911), while considering Chamaeleontidae the valid family name, recognized *Chamaeleon* (=*Chamaeleo*) *pumilus*, but not *M. pumila*. Matthey (1931) and Matthey & Brink (1956, 1960) applied cytological technique to what they regarded as chamaeleontids. They found male chamaeleons have no 'Y' chromosome, and showed that *Microsaura* should not be considered apart from *Chamaeleo* and that only one species (*pumilus*) was valid. Skinner (1958) noted the shoulder girdle of *Microsaura pumila* (=*Chamaeleo pumilus*) was more like that of *Chamaeleo* than that of *Brookesia*.

Hillenius (1959, 1963) has reviewed the genus *Chamaeleo* from morphological considerations and co-ordinated these with the cytological findings of Matthey (1931) and Matthey & Brink (1956, 1960). As far as the *pumilus* group is concerned, these workers agree that: (1) *Microsaura* is invalid and referrable to *Chamaeleo*. (2) There seems to be one species, *Chamaeleo pumilus*, and the other *Microsaura* species and/or subspecies (e.g. *caffer*, *damaranus*, *gutturalis*, *karrooicus*, *melanocephalus*, *occidentalis*, *taeniobronchus*, *transvaalensis*, and *ventralis*) are best considered no more than subspecies of *Chamaeleo pumilus* until more detailed studies indicate the contrary. Furthermore, *C. p. pumilus* of the southern Cape Province has more characters in common with *C. melanocephalus* than with its subspecies *C. pumilus transvaalensis*. *C. p. transvaalensis* shares more characters with *C. v. ventralis*, *C. ventralis occidentalis* and *C. damaranus* than with *C. p. pumilus*. The hemipenes of *C. pumilus* are of the 'cogwheel' type as in *C. dilepis* (Broadley 1971). The viviparous South African *C. pumilus* group is distinct from the viviparous East African *C. bitaeniatus* group. Therefore, there is no validity in the arguments of Methuen & Hewitt (1913) and Power (1932) for re-establishment of a separate genus (*Lophosaura* and *Microsaura* as per Gray, 1864).

Hillenius (1959, 1963, 1964) investigated distribution of characters, not of species, and showed that East Africa has the greatest number of characters, and, hence, is the origin of *Chamaeleo*, with secondary centres in Madagascar and West Africa. Away from East Africa the number of shared characters diminishes. Thus, while Madagascar has the bulk of chamaeleonid species and the greatest variety of form and size, it is not the original home of *Chamaeleo*, and chamaeleonids flourish there because of the absence of higher predators as well as competitors. Hillenius (1959, 1963) showed that earlier taxonomists wrongly assigned characters as 'key' because they had not studied the whole group and often recognized species on few specimens, or even one, and in some cases confused sexual dimorphism with their 'key' characters, which they often did not apply uniformly, assigning females to one genus or species and the males to another. Mertens (1966) endorses Matthey's (1931), Matthey & Brink's (1956, 1960) and Hillenius's (1959, 1963, 1964) views in determining subdivisions of the form-rich and unwieldy *Chamaeleo*, and hopes the procedure will be extended to *Brookesia* to better understand taxonomic relationships within the chamaeleonids (or chamaeleontids). Mertens agrees recognition of *Microsaura* is unwarranted until a study of all forms is made, and currently validity of *Microsaura* cannot be recognized on purely nomenclatural views alone. Mertens feels a study of the *pumilus* and *dilepis* complexes will raise rather than diminish the 113 species of *Chamaeleo*. For this investigation, the nomenclature of Daudin as validated by Hillenius and Matthey is endorsed.

A. Smith (1831) originally described the Namaqualand chamaeleon as *Chamaeleo namaquensis*. Fortunately, *C. namaquensis* is harder to find than other chamaeleons, thus largely escaping the taxonomic confusion perpetrated on *C. pumilus*. After several questionable changes, Gray (1864) finally placed *namaquensis* in its own genus, *Phumanola*. Werner (1911) placed *namaquensis* in *Chamaeleon*. FitzSimons (1943), Hillenius (1959, 1963) and Mertens (1955, 1966) call it *Chamaeleo namaquensis*. Hillenius (1959) feels that *Chamaeleo namaquensis*, while previously considered as very isolated and not closely related to other species, is in fact more or less related to the *Chamaeleo chamaeleon* group in homogenous squamation, sometimes with scales in rosette-shaped groups, no temporal crest, casque as *Chamaeleo basiliscus* (roof-shaped parietal crest higher than lateral crests, elevated posteriorly, lateral crests stopping just after the temporal region, no occipital lobes). *Chamaeleo namaquensis*' dorsal knobs are very similar to those of the Camerounian *Chamaeleo wiedersheimi*, whose position is unknown because of insufficient material, but is similar to *Chamaeleo namaquensis* in several characters. Since *Chamaeleo dilepis* is in the *Chamaeleo chamaeleon* group, its link with *Chamaeleo namaquensis* makes sense from the point of distribution.

B. *Distribution and habitat*

Chamaeleo pumilus is of southern African distribution, occurring from Lüderitzbucht, South West Africa (ignoring an introduced population at Walvis Bay), south through the Cape Province and north through Natal to the north-east Transvaal (FitzSimons 1943, 1965; Hillenius 1959; Mertens 1955, 1966). For an arboreal chamaeleon it is of ubiquitous habits and habitat, inhabiting the extremes of desert shrubs of Namaqualand and the Karoo and the high rainfall areas of the south-east coast and Drakensberg plateau.

Chamaeleo namaquensis ranges from southern Angola through South West Africa from the Atlantic shore to the east of the Great Western Escarpment and south through karoid parts of the Cape Province (FitzSimons 1943; Hillenius 1959; Mertens 1955, 1966). It inhabits arid and semi-arid situations, some of which seem an unlikely 'chamaeleon' habitat. One of the few ground-dwelling chamaeleons—*Brookesia* of Madagascan tropical rain forests is another—it is one of two chamaeleons to invade strict desert. The other deserticulous chamaeleon is the ubiquitous Mediterranean variety (*Chamaeleo chamaeleon*), to whose group *C. namaquensis* is probably related. Alexander's (1838) description of *C. namaquensis* at Walvis Bay still holds true for an introduction: 'When [approached] these cameleons [*sic*] . . . opened their mouths . . . and bissed like angry snakes, whilst a bag under their mouth swelled to a great size, which, with their dark blotched bodies, gave them a hideous appearance. They run fast, and are accounted to be poisonous by the natives.' Alexander's description is correct, for they can run at a quick walk and their high speed evasions make flight a satisfactory escape for this chamaeleon.

This study was largely motivated by the virtual dearth of knowledge on chamaeleon ecology. In essence, this paper presents two autecological studies on the mesic-adapted *Chamaeleo pumilus* and the xeric-adapted *C. namaquensis.* The problem of the role of body compression and colour change was investigated in the field and in the laboratory, as was the dynamics of chamaeleon physiological thermoregulation in maintaining these animals in thermal equilibrium with their respective environments. A study of chamaeleon habitats was undertaken to see if they were of ubiquitous or restricted habitat preferences. The reproduction of the oviparous *C. namaquensis* and viviparous *C. pumilus* was thoroughly investigated under natural conditions and supplemented with laboratory records. A complete idea of chamaeleon reproduction was acquired from courting to maturity of the young. The reproductive potential was integrated with field studies on mortality, population dynamics, spatial organization, and behaviour. A detailed investigation was made on nutrition needs and prey items, and water and salt metabolism. The last study was particularly interesting, since *C. namaquensis* inhabits the desert littoral, ingesting food of high salt content, the salt being excreted via a nasal salt gland. The study of adaptation to desiccation in both chamaeleons provided valuable information on their respective solutions to water balance and water sources.

After preliminary field studies on chamaeleon requirements, conditions for successfully maintaining captives were improved, allowing laboratory findings to complement field studies. Since captive chamaeleons usually do poorly, this casts considerable doubt on the acceptance of previous findings on captives. Thus, in this study an attempt was made to integrate laboratory and field investigations to give as complete an understanding of the ecology and environmental adaptations of at least two chamaeleonids.

II. Materials and Methods

A. *Collecting and observational methods*

Specimens of *Chamaeleo pumilus* were collected and observed from 13 January 1969 to 30 November 1970, chiefly at Stellenbosch, but also at Beaufort West, The Strand, Van der Stel, and in the Cape Peninsula in the Cape Province. They were readily found on garden shrubs, bushes, grasses, and on reeds along the margins of various bodies of water in developed and undeveloped areas.

Specimens of *C. namaquensis* were observed and collected during 1969 in April, June, August and November, and in February 1970 in South West Africa. Inland populations of *C. namaquensis* were investigated at Gobabeb, Tsondab, Geluk Farm, Solitaire and Rehoboth, and coastal populations from Walvis Bay north to Cape Cross.

C. pumilus and *C. namaquensis* would not enter any sort of trap, requiring employment of random and sector search methods. In the latter method, a given area was intensively searched in the morning, collecting, taking data from the animals present, while noting signs and marking the site. The afternoon search sector was reached by walking to it via the morning sector, checking on the markers to see any fresh signs or, hopefully, the animals themselves. This method proved quite rewarding. These patrols were more or less straight lines and selected through varied habitats. Return was by a parallel route. The maximum daily return distance covered was 25,75 km, the minimum 12,88, the average 19,31. Shorter trips with observation points were also employed, especially for social interaction, activity, and territorial studies. The sites to which animals were retreating for the night were marked on the return afternoon sector search, for later observations during the night. Binoculars were employed for observing both species from a distance.

Animals were marked by branding an identity number on the proximal ventrum of the tail, or by small identity number-bearing leg bands. Chamaeleons were first cooled to render them comatose, and restrict peripheral circulation to minimize bleeding when the number was applied with a sterilized surgical blade. Both methods were durable and effective. A total of 165 (87 ♂♂, 78 ♀♀) coastal and 42 (22 ♂♂, 20 ♀♀) inland *Chamaeleo namaquensis* adults were marked, and 107 coastal juveniles. A total of 494 (159 ♂♂, 187 ♀♀, 148 juveniles) *C. pumilus* were marked at Stellenbosch. These animals were never killed or collected, serving as subjects for field territorial, behavioural, and reproduction studies. Reproduction data were obtained by palpating. Prey preferential studies were also gathered from them by observation and scat analysis.

B. *Thermal studies*

A Wesco rapid equilibrium cloacal thermometer was used to obtain most lizard field temperatures, though a Yellow Springs Instrument 46TUC Telethermometer (probes YSI 402 body; 405 air temperature; 409 skin surface; 524 subdermal) was employed, occasionally in the field, and exclusively in all laboratory studies on thermoregulation, metabolic, and cardiac rates. Since colour change of chamaeleons is rapid and alters the skin temperature, all skin temperatures must be recorded as rapidly as possible. The telethermometer is the superior instrument, since it records temperatures almost instantly, and several probes can make simultaneous recordings. However, by simultaneously calibrating telethermometer readings with those made by a thermometer, a technique was devised to reflect most accurately all chamaeleon temperatures. All skin temperature readings (first, side to the sun; second, side in the shade) must be made as soon as possible, and precede cloacal readings. The skin surface temperatures must be made in such a manner that the chamaeleon is not greatly alarmed. For example, a pale chamaeleon on a hot day is reflecting heat, and the temperature of the skin presented to the sun is at or near that of the air temperature. If angered, such a chamaeleon goes uniformly black in less than 1,6 seconds, and almost instantly absorbs heat ($\geqslant$3,0 C rise in skin surface temperature within 30 seconds). *Chamaeleo namaquensis* and *C. pumilus* did not evince more than alertness if approached slowly and skin surface temperatures recorded gently. Though the cloacal temperature lags in reflecting the skin surface temperature, all cloacal readings must be made within 10 seconds of capture, and all readings employing a cloacal thermometer must be completed within 20 seconds, cloth insulating the chamaeleon during the reading to eliminate temperature exchange between the investigator and subject. All chamaeleon and environmental temperatures were recorded in the shade of the author's body. Data were not used from injured chamaeleons, those forced to remain in the shade or open by the author's activity, or those that were not readily captured or overtly disturbed.

Various substrate and air temperatures were recorded in the field to assess their bearing, if any, on chamaeleon body temperatures. Surface substrate temperatures were taken by resting the recording instrument on the surface. Temperatures at subsoil depths of 0,5; 2,0; 5,0; 10,0; 15,0; 20,0; 25,0 and 30,0 cm were taken by pushing the recorder down until the desired depth was reached. Air temperature was taken at two metres (T_a2m) and fifty millimetres (T_a50 mm) from the substrate surface, or what the animals were on. Environmental temperatures (T_e) were the same as the T_a50 mm reading in the case of *Chamaeleo pumilus*. Environmental temperatures in the case of *C. namaquensis* varied according to what the animals were on (rock, gravel or sand surfaces), the vegetation-protected temperature of the substrate surface (T_s), the vegetation-protected T_a50 mm when in or on a plant, and the T_s of the lee, crest, or windward of hummocks. Details of weather, cloud cover, wind velocity and direction, and sunrise and sunset were also recorded. All such weather data collected from 13 January 1969 to 30 November 1970 were divided into 'cool' (April to September) and 'warm' (October to March) months, and further subdivided into 'fair' (0–29% cloud or fog), 'overcast' (29–100% cloud or fog), and 'rainy' weather lasting throughout the day. For coastal Namib readings, the condition of early morning and late afternoon fog with clear midday skies, necessitated the category of 'partly overcast'.

A laboratory experiment of thermoregulation was designed to test the role of body compression and skin colour in light and total darkness. A light-proof temperature room (effective ambient temperature: −5,0 to 40,0 C) was used, so that the animals could be tested over the same temperature range in total darkness and in light, and in light followed by dark and so on sequentially. Radiant heat and light from a uni-directional source, as with the sun, was employed, except in dark conditions when just heat was used. Ten animals of each species, two at a time (one of each species), were secured by tape to a board (160 × 70 mm) in such a manner that they could compress and position the body freely and stand up, stiff-legged, but not walk off. The board and the animals were supported by a ring stand 300 mm from the counter surface. Thirty-minute intervals at each temperature (−4,5; 2,5; 5,7; 15,0; 17,0; 18,0; 25,0; 30,0; 35,0; 42,0 C with light) (−5,0; 5,3; 8,6; 12,0; 13,8; 14,6; 20,3; 23,0; 30,1; 40,0 C in the dark) were used to conform with previous colour studies, though results at ten-, twenty-, and sixty-minute intervals were virtually identical. Trial runs were conducted for a week to allow the subjects to become accustomed to the protocol. In the dark, instrument readings were made with a flashlight, screened from the subjects. Ambient air temperature, skin surface and chamaeleon body temperatures were recorded at each time interval, along with notes as to body compression, skin colour, and behavioural state of the subjects.

A second temperature test was set up in an outside enclosure (3 × 2 m) to examine body compression and skin colour in thermoregulation under 'natural' conditions. The floor was red Namib dune sand 150 mm thick in which was embedded a pot containing a small acacia plant. Ten specimens each of *Chamaeleo namaquensis* and *C. pumilus* were used. The plant was provided for *C. pumilus*, which will not climb down from, and is at ease when a raised object is available. Adult *C. namaquensis* will not climb. Substrate temperatures were recorded as well as the readings made in the previously described experiment. Telethermometer leads were made sufficiently long enough to allow the animals complete freedom of movement and action. Data from two animals of each type could be recorded simultaneously. Five days were allowed for the subjects to become accustomed to the set-up, followed by ten days of data-taking. Suitable precautions were taken to allow as many animals as possible to be used without causing territorial stress that would affect colour and compression changes.

Preferred temperature tests were run on both species (18 *Chamaeleo namaquensis*, 20 *C. pumilus*) at ambient temperatures of 5,0 to 50,0 C in long, runway-type cages 3×2 m which were placed horizontally for *C. namaquensis* and vertically for *C. pumilus*, in order to house a small potted plant for the convenience of the latter. Red Namib dune sand arranged in banks of various depths (50–300 mm), and scattered rocks provided shelters. Thus, by such arrangements, spatial behaviour of both forms was also realized. Instrumentation and readings recorded were as in the previously described experiments. Preferred temperature tests were run for two weeks, after allowing the subjects a week to get used to the arrangement and select space preferenda.

The role of the skin in mediating core temperature changes in chamaeleons was examined at various ambient temperatures from 5 to 35 C at 10 degree intervals. Water blebs were injected subdermally in ten *Chamaeleo pumilus* and eight *C. namaquensis* and subdermal thermistor probes inserted on both sides of the body of each chamaeleon and another probe inserted into the large intestine of each subject. Skin surface, subdermal, body, substrate, and air temperatures were then read from the telethermometer at a given temperature interval, and the colour of both sides of the body, body compression, and other notations recorded. The same test was run on five dead and five live individuals of each species to assess heating and cooling rates at a given temperature in live and dead chamaeleons.

C. *Metabolic rate studies*

A device as described by Bailey, Kitts & Wood (1957) was employed and their procedure followed, except that the equilibration time was lengthened to thirty minutes. The value of this device is the ease with which oxygen consumption can be measured at various activity levels over any time interval.

Chamaeleons struggle violently if restrained in a submerged vessel, so telethermometer leads were made sufficiently long enough to ensure maximum freedom of movement. Readings at rest were possible, and since the subjects periodically sought active escape, various activity states could be measured, such as torpor, sleep, awake but alert, and active. The animal vessel was provided with a small twig for the convenience of *C. pumilus*.

Oxygen consumption from 5,0 to 45,0 C was measured, and apart from 40 to 45 C, ten degree temperature intervals were employed. Recording instrumentation for temperatures was as in the previously described thermoregulation experiments. Air temperatures of both the animal and blank vessels were recorded, as well as the body temperatures of the animals. Also recorded were the respiration rates, body compression, and skin colour of the animals, and when they commenced panting. At temperatures other than 20 C, a nearby oven and refrigerator were used to hold, raise, or lower subjects' temperatures to the test level. A period of 205 minutes was necessary to bring *C. namaquensis* body temperatures down from 20 C to 5,0 C and 100 minutes for *C. pumilus*. Sixty minutes were needed to raise *C. namaquensis* body temperatures from 20 to

40 C and 35 minutes for *C. pumilus*. Difficulties were encountered bringing *C. pumilus*, except for two, to 45 C. Fifteen *C. pumilus* ranging from 5,1 to 24,7 g ($\bar{x}$ = 11,4); and 15 *C. namaquensis* ranging from 49,3 to 113,4 g ($\bar{x}$ = 76,1) were used. Rehearsal runs were conducted for a week to allow subjects and experimentor familiarization with technique and equipment. Recordings were made from 08:00 to 18:00 hours, with test temperatures temporally varied to eliminate any circadian rhythm effects. Results were corrected to standard temperature and barometric pressure.

D. *Cardiac rate studies*

The relationship of chamaeleon heart rate to temperature was also investigated. Five *C. namaquensis* (71,6–115,0 g; $\bar{x}$ = 80,0) and five *C. pumilus* (6,0–26,0 g; $\bar{x}$ = 13,0) were used. Ten degree temperature intervals from 5,0 to 45,0 C were employed, animal body temperatures being held, raised, or lowered as previously described. During experimental runs, a pan containing ice was placed under the subjects to keep ambient temperatures low, and a red lamp 0,5–1,0 m away was employed for higher temperatures. A small twig was necessary for the *C. pumilus* to cling to. The animals were placed in a container 660×300×300 mm open to the experimentor on one side. Body and air temperatures were monitored as in the previously described experiments, and a Stanley Cox Electrocardioscope (Med 158) recorded heart beat. Familiarization runs were conducted for a week for the specimens to become used to the procedure.

E. *Food studies*

In calculating the amount devoured by 25 captive *Chamaeleo namaquensis*, 35 captive *C. pumilus*, and chamaeleons in the field, food was measured by volumetric water displacement and arranged by size from very small (< 0,25 ml; 2–3 mm long), small (0,25 ml; 10 mm long), medium (0,75 ml; 20 mm long), large (2,0 ml; 30 mm long), to extra large (4,5 ml; 54 mm long), respectively Food Indices 1–5. Marked prey was given to chamaeleons at different times to determine rates of passage.

Prey taken by wild chamaeleons was studied by sacrificing the following: *C. pumilus* (February, 6 ♀♀, 3 ♂♂; March, 6 ♀♀, 6 ♂♂; April, 9 ♀♀, 8 ♂♂; May, 8 ♀♀, 8♂♂; June, 10 ♀♀, 6 ♂♂; July, 10 ♀♀, 5 ♂♂; August, 7 ♀♀, 8 ♂♂; September, 7 ♀♀, 5 ♂♂; October, 7 ♀♀, 3 ♂♂; November, 5 ♀♀, 5 ♂♂; December, 6 ♀♀, 4 ♂♂; January, 5 ♀♀, 4 ♂♂; 1969–1970), and *C. namaquensis* (April, 9 ♀♀, 5 ♂♂; June, 14 ♀♀, 9 ♂♂; August, 5 ♀♀, 4 ♂♂; November, 11 ♀♀, 6 ♂♂; February, 11 ♀♀, 6 ♂♂; 1969–70). Animals were collected in the morning and afternoon when they were adjudged to have eaten, but not yet digested their meal. Chamaeleons were killed by decapitation and then preserved in 70% alcohol, with exact date, time, and locality. Length of the stomach, small and large intestine were measured in millimetres with Vernier callipers or measuring dividers. Stomach contents were removed, weighed on a Mettler H10T balance and placed in vials with identifying labels for future analyses. Scats provided a valuable source of prey information for both species, particularly *C. namaquensis. C. namaquensis* scats are large (up to 60 mm long) and very distinct. They last in the wind and shifting sands for about three days, though only those no more than two days old were taken. Fresher ones formed the bulk of scats examined. Scats were collected and processed in the manner previously described for stomach contents. The percentage of items in stomach contents and scats was calculated by volumetric analysis. Endoparasites were also removed from the digestive tract, placed in 70% alcohol and sent to Dr Prudhoe of the British Museum (Natural History) for identification.

F. *Water and salt balance studies*

Ten *Chamaeleo namaquensis* (17,8–90,1; $\bar{x} = 58{,}1$ g) and ten *C. pumilus* (6,4–12,4; $\bar{x} = 9{,}2$ g) were fasted but hydrated for 24 hours prior to use in a desiccation study. They were then weighed on an Ohaus animal scale and placed one each in glass desiccation chambers (0,20 m diameter) in zero per cent humidity created by silica blue gel crystals below and separated from the animals. The lips of the chambers were sealed with silicon grease. A small twig, pre-dried in an oven, was provided for the *C. pumilus* to cling to. The test was run for seven days at 25,0 C ±1,3 in a temperature room, the chamaeleons subjected to eight hours of light per day. Faeces and uric acid were removed daily and weighed (Mettler H10T balance). Wastes were removed early in the morning at such time when fasting chamaeleons always had eliminated. Each chamber was aerated daily. At the end of seven days, all animals were weighed and a half of each species group were killed. Blood samples were taken from this dehydrated group in haematocrit capillary tubes and centrifuged on a clinical centrifuge at 2 500 rpm for thirty minutes. A second blood sample, taken in polyethylene microtest tubes, was centrifuged at 10 000 rpm for five minutes to obtain plasma for freezing point determination of osmolality. The remainder of each species were given as much water as desired and the following day weighed and killed, the previously described procedure for the dehydrated group being followed.

A separate study lasting twelve days examined survival with food but no water. The animals were placed in a separate cage maintained at 25,0 C ±3,2; and 40–50% humidity. Eight *C. pumilus* (6,1–14,9; $\bar{x} = 9{,}7$ g) and seven *C. namaquensis* (36,0–91,4; $\bar{x} = 61{,}7$ g) were weighed at the start, every third day and at the conclusion of the study. Faeces and uric acid were collected as soon as they were eliminated and weighed as previously described, and blood and plasma taken as previously from two *C. pumilus* and two *C. namaquensis* on the twelfth day. The survivors were dehydrated and body weights taken daily as were the weights of any droppings. At day 15 the survivors were killed, being processed as previously described.

Blood was similarly taken from seven freshly caught *C. pumilus*, and seven inland and ten coastal *C. namaquensis* for haematocrit and osmolality plasma determinations. For *C. pumilus* analysis was immediate, but for *C. namaquensis*, except for haematocrits, analysis was one to three days after capture.

The osmolality of chamaeleon plasma was determined by measuring the comparative melting point against standard solutions (100; 325; 500 and 900 mOsm) in the manner of Gross (1954).

The exudate from the nares of *Chamaeleo namaquensis* suggested the presence of a nasal salt gland, the nature of which was grossly examined but not so histologically. An exudate sample was examined by Dr V. Wolfe, Department of Chemical Pathology, University of Stellenbosch, using a flame photometer.

G. *Territorial and population studies*

The method employed for the iguanid *Uta stansburiana hesperis* (Burrage 1966) was adapted for chamaeleon territorial studies and was especially valuable for *Chamaeleo namaquensis*. This method allows territorial investigations and population structure to be studied together. Close daily observation throughout the day gave an accurate picture of the spatial arrangement of chamaeleons, not only in regard to the extent of the territory of individuals, but also those parts most used. The open desert facilitated distant observations by binoculars from a vantage site. Points visited by a chamaeleon were marked at the site, the lizard's number, sex, and date being printed on a marker in waterproof ink. The points were simultaneously plotted on a scaled map on graph paper of the given area. The denser the dots, the greater the activity of the lizard within a given part of its occupied area, and the peripheral dots on the map and site markers gave the exact area. Connecting the outlying dots gave the periphery of the territory, the area of which was then computed with a planimeter from the graph paper. Territorial conflicts and social interactions were marked on the site on which they occurred and on the graph paper to determine usage of a given territory and which part(s) were most vigorously defended.

H. *Reproduction studies*

Those *Chamaeleo pumilus* and *C. namaquensis* used in food studies also served for anatomical examinations of reproductive state. Each chamaeleon was tagged with the date, precise locality of collection, and observational data. Chamaeleons were weighed on a Ohaus animal scale and then killed, whereupon various measurements were taken with measuring dividers. All *C. pumilus* and most *C. namaquensis* were freshly dissected and their reproductive structures studied. Those *C. namaquensis* not studied immediately after death, were stored in 70% alcohol. The maximum delay in examination was seven days. The chamaeleons, their reproductive structures, embryos (*pumilus*), eggs (*namaquensis*) were measured with Vernier callipers or measuring dividers in millimetres. The reproductive structures were weighed on a Mettler H10T balance. These excised parts were fixed in 10% and preserved in 4% formalin. Routine histological techniques were carried out on some of these reproductive tissues which had been embedded in paraffin wax. Sections were cut to 5 or 8 μ and stained with haematoxylin-eosin, or azo-carmine and azan.

In order to examine the role of the fat bodies in reproduction, a group of six *Chamaeleo pumilus* and four *C. namaquensis* females and four males of each species had their fat bodies excised. Four controls in each species category group were sham-operated. The animals were cryo-anaesthetized and kept comatose during the operation by being placed ventrum up on a plastic bag filled with crushed ice in which was moulded a hollow to accept each subject. Sterile instruments and technique were employed. Cautery sealed the severed areas, and sterilized adhesive 'butterflies' closed the wounds.

In order to examine the role of the corpora lutea, five pregnant female *Chamaeleo pumilus* had their corpora lutea excised, with another five sham-operated as controls. Four gravid *C. namaquensis* had their corpora lutea excised, with an additional four sham-operated as controls. The operative technique was as previously described for fat body excision.

III. Results and Discussion

A. *Habitat of Chamaeleo pumilus*

Chamaeleo pumilus inhabits any vegetation guaranteeing a plentiful and sustained prey source, such as flowering bushes and hedges, grasses, supratidal bushes and grasses, and especially reeds surrounding stagnant bodies of water. *C. pumilus* was observed in the Cape Province, in the southern Namib Desert at Port Nolloth, the semi-arid Karoo at Leeu-Gamka and Beaufort West, and the south-west Cape winter rainfall area at Stellenbosch, Van der Stel station, and The Strand. The vegetation at Port Nolloth is West Coast Strandveld, consisting of open, semi-succulent scrub of Fynbos form and intermediate between the Coastal Fynbos and the Succulent Karoo. The Karoo vegetation is complex, consisting of succulents, and semi-arid shrubs. The winter-rainfall area has evergreen shrubs, with a variety of grasses and other annuals. A full discussion of the vegetation of all these areas is given by Acocks (1953).

B. *Description of study stations of Chamaeleo pumilus*

Stellenbosch is situated in gently rolling lowland at the mouth of the Jonkershoek Valley. Data were taken from *Chamaeleo pumilus* inhabiting the University of Stellenbosch Botanical Gardens, suburban hedgerows and gardens, which are planted with many exotics, and from the Marais Park with natural shrubs. *C. pumilus* was also studied in vegetation surrounding freshwater bodies, roadside and railroad right-of-way ditches (Fig. 1), where reeds, mostly *Phragmites*, predominate. Van der Stel station and The Strand occupy inland and coastal situations respectively, on the gradually seawards sloping base of the Hottentots Holland range. *C. pumilus* is abundant in the reeds along the railroad right-of-way at Van der Stel station, and supratidally on the backshore shrubs and grasses at The Strand.

Weather data for the principal study station of Stellenbosch are presented in Table 1, from data provided by the Geography Department of the University of Stellenbosch. During 1969–70 rainfall was approximately two-thirds normal, though the preceding years had average precipitation. Stellenbosch has a winter-rainfall climate with the bulk of the rain falling in winter, though not entirely limited to it. North-west winds bring rain; south-westerly clearing with showers to fine; south-easters are strong winds.

Table 1. Weather data for Stellenbosch, Cape Province, Republic of South Africa (source, Geography Department, University of Stellenbosch). Temperatures are in degrees Celsius; rainfall in millimetres.

	Temperatures					
	Absolute		Mean		Monthly	
	Max.	Min.	Max.	Min.	Mean	Rainfall
1969						
January	33,7	8,5	26,0	13,2	19,6	41,9
February	36,0	9,4	28,1	14,3	21,2	23,5
March	41,1	9,5	27,6	14,4	21,0	38,5
April	26,6	4,1	20,9	10,3	15,6	45,9
May	26,0	3,5	20,1	6,6	13,3	17,1
June	26,6	1,7	16,6	6,4	11,5	91,3
July	25,6	1,0	16,5	5,1	10,8	71,9
August	29,4	2,0	18,2	7,0	12,6	85,6
September	28,9	1,0	18,0	5,6	11,8	88,4
October	34,4	6,5	20,5	9,9	15,2	66,1
November	33,3	6,0	24,0	10,2	17,1	16,7
December	36,7	7,0	27,3	12,8	20,0	8,0
1970						
January	37,8	10,1	28,5	13,9	21,3	8,9

The native vegetation is macchia shrub of Coastal Rhenosterbosveld (Acocks 1953), of which rhenosterbos (*Elytropappus*) is distinctive. There is a variety of undershrubs, grasses, and other annuals. On beaches and disturbed areas succulents such as *Mesembryanthemum* predominate. Over the years much native vegetation has been destroyed and the area planted with exotic trees.

Reptiles preying on *Chamaeleo pumilus* are discussed in the predation section (see p. 32), and this discussion deals with co-inhabiting reptile competitors of *C. pumilus*. The most important reptilian competitor of *C. pumilus* is the skink *Mabuya capensis*, which is of ubiquitous habits and, while primarily ground-dwelling, frequently ascends into and hunts prey in shrubs inhabited by chamaeleons. It appears less in evidence in grassy and reedy areas, where it does not climb into such vegetation. A large skink might prey on any newborn *C. pumilus* encountered. *C. pumilus* was rare in exotic montane conifers, but was common in such trees in lowland areas. Montane conifers are abundantly inhabited by geckos (*Phyllodactylus*), which might prevent *C. pumilus* from successfully invading this niche. However, montane areas might represent marginal habitat to *C. pumilus*, since the largest concentrations of chamaeleons in uplands were limited numbers on shrubs on sunny slopes and streamside vegetation.

Fig. 1.

Chamaeleo pumilus habitat on reeds, mostly *Phragmites*, growing in ditch beside railroad right-of-way (Stellenbosch goods yards).

C. *Habitat of Chamaeleo namaquensis*

Mr John Visser found a large *Chamaeleo namaquensis* on the road near Laingsburg, Cape Province, and it is recorded from the arid and semi-arid (Fig. 2A) portions of the Cape Province. The author studied them in the most arid part (that between 18° to 29° South latitude) of the central Namib Desert (Meigs 1966) of South West Africa along the coast from Walvis Bay north to Cape Cross, in the interior at Gobabeb and Tsondab, the edge of the Great Western Escarpment at Geluk Farm and Solitaire, and the South African Plateau highlands at Windhoek and Rehoboth. The geography and other vitae of this area are given by Meigs (1966), Koch (1961), Logan (1960), Schulze (1969) and the *South West Africa handbook* (1971–2); the first three containing pertinent literature to more detailed studies. The plateau and Great Western Escarpment are better-watered, supporting grasses and scattered thorn trees (Fig. 2B) on the uplands and steppe along the escarpment. Vegetation rapidly becomes sparser farther west to the Atlantic, and in the true Namib is meagre and may be absent. Around mountains, and along watercourses the 'luxuriance' of vegetation varies according to the water supply from riverine forest along the Kuiseb River to a better showing of succulents along washes.

D. *Description of study stations of Chamaeleo namaquensis*

The principal study areas were the coastal central Namib Desert from Walvis Bay to Cape Cross, based at Swakopmund, and the interior, based at the research station at Gobabeb, 120 km south-east of Walvis Bay and about 58 km from the Atlantic. Sorties were made to surrounding areas from these bases. General descriptions of these regions are given by Logan (1960), Koch (1961) and Meigs (1966). Dunes, mountains and gravel plains are the principal biotopes, with special biotopes of hygrophilous or halophilous strata, for example, river beds and pans.

That part of the littoral Namib (Fig. 5A) studied is primarily sandy beach with occasional outcrops of the underlying Namib bedrock platform, and massive deposits of fly-infested tidal wrack. The backshore is a monotonous expanse of soft, dirty gray-white gravel, virtually devoid of plants. South of the Swakop River are dunes lying east of the coastal rail line, over which they occasionally drift. Proximal to the beach are small (about 10 m high), whitish gray seif dunes devoid of vegetation. Further inland, especially near Walvis Bay, the coastal dunes (Fig. 6A) are considerably larger (about 200 m high), yellow, and support sparse vegetation.

The north bank of the Swakop River consists of barren, flat-topped limestone bluffs (Fig. 6B). The base of this outcrop has a skirting deposit of wind-blown dune sand. Away from the outcrop is the monotony of the featureless gravel plains (Fig. 5B) unbroken except for slightly indented meandering washes. Farther north the monotony of the gravel plain is broken by broad-based, narrow-ridged outcrops of black diorite and white dolomite. South of the Swakop River gravel plains form corridors between dune ridges.

The Swakop River bed (Stengel 1964) consists of river channel, flats (Fig. 4B) and varied sized hummocks (Fig. 7A) of whitish sand. These river hummocks may be single or inter-connected as a miniature mountain range. Stengel's Map 1 graphically shows the area of dune hummocks (Fig. 7B) in the Swakop River bottomlands, which mostly lie south of a 1,3 m high bank and the coastal dunes. These hummocks are composed of wind-blown dune sand and are of varied size, but not as large as the river hummocks, nor interconnected. Dune hummocks reach a maximum height of 2,3 m and river hummocks 3,5 m.

At the principal central Namib Desert interior site of Gobabeb are located featureless gravel plains, with occasional granitic outcrops (Fig. 3A), large reddish dunes (Fig. 3B), with basal vegetation (mostly *Aristida* grasses), the riverine forest of the Kuiseb (Fig. 4A), granitic mountains (Fig. 3A), such as Zwartbank and Rooikop, and sandy flats, with scattered grass clumps. Further descriptions of the physiography are given by Logan (1960), Koch (1961) and Meigs (1966).

Table 2 gives air and substrate temperature data for the coastal and interior central Namib and is derived from data collected by the author, those collected at Swakopmund by Mr Moisel for the Namib Desert Research Station, and by the Namib Desert Research Station at Gobabeb for the interior. These data are in addition to those made for environmental and body temperatures collected for the chamaeleons, and thus there are some differences. According to the *South West Africa handbook* (1971–2), Swakopmund has an average yearly precipitation of 16,2 mm over 40 years of records; heavy rains

Figs 2–7.

Habitats of *Chamaeleo namaquensis*. Leeu-Gamka, Cape Province is also a habitat of *C. pumilus*. All other photographs were taken in South West Africa.

Fig. 2A.

The Karoo in the region of Leeu-Gamka, Cape Province, Republic of South Africa.

Fig. 2B.

Scattered thorn trees on grassland of South African Plateau in vicinity of Rehoboth.

Fig. 3A.

Outcropping of white weathered marble and black dolerite, Zwartbank Mountain, breaks featureless gravel plain of Namib Outer Platform.

Fig. 3B.

Base of large, red inland dune near Gobabeb, showing heavily overgrazed *Aristida sabulicola* hummock in right foreground. Hummock in left centre is a 'narras' (*Acanthosicyos horrida*).

Fig. 4A.

Kuiseb River bottoms with *Eragrostis spinosa* grass and *Acacia giraffae* and *A. albida* trees in the background. Large dunes form backdrop.

Fig. 4B.

Mud-cracked channel in stream-deposited gravel flats of the Swakop River. In the right centre is a *Chamaeleo namaquensis*. Nasal salt exudate appears as a small white spot on the chamaeleon's nose.

Fig. 5A.

Namib littoral at mouth of Swakop River, showing deposits of tidal wrack and other debris. *C. namaquensis* forages seawards at least to the tidal wrack.

Fig. 5B.

Featureless gravel plain near Swakopmund forming a street between dunes. Small *Zygophyllum stapffii* bush just visible at foot of dunes at right.

Fig. 6A.

Near Swakopmund, vegetationless coastal dune, on lee slope (slip-face) of which a chamaeleon was discovered with body temperature of 34,2°C (sand surface temperature, 67,0°C).

Fig. 6B.

Limestone outcrop on north bank of Swakop River, showing its barren flat-top. Small black dots are plants.

Fig. 7A.

River hummocks in bottomlands of Swakop River. Note inter-connected nature and larger size of this hummock type. *Eragrostis spinosa* grass forms partial cover.

Fig. 7B.

Dune hummock region. Predominant hummock vegetation is *Eragrostis spinosa* grass, *Trianthema* sp. and *Zygophyllum stapffii*. A single *Nicotiana glauca* is in right foreground; *Tamarix austro-africana* in left background on foot of dune, and a 'narras' (*Acanthosicyos horrida*) on foot of dune in distant left centre.

Fig. 2A.

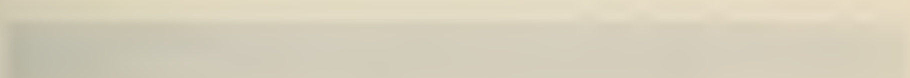


Fig. 2B.

Fig. 3A.

Fig. 3B.

Fig. 4A.

Fig. 4B.

Fig. 5A.

Fig. 5B.

Fig. 6A.

Fig. 6B.

Fig. 7A.

Fig. 7B.

of 42,1 mm fell in 1969, with 41,3 mm falling in March alone, and as little as 0,4 mm in 1959. The Namib Desert has very little rain of erratic distribution, the causes of which are reviewed by Logan (1960) and Meigs (1966). Inland areas are both wetter (more rain) and drier (lower humidity) than coastal locales. Fog is a persistent and normal feature of the Namib Desert, especially along the coast, but its effect reaches far inland (at least 200 days per year, 58 km from the coast). The moisture realized from fog far exceeds that from rain, as demonstrated by Walter (1937), who in one month collected more than 250 litres of water condensed from fog on the inclined roof (60 m^2 in area) of a house in Swakopmund. The immense, similarly inclined plane of a dune must collect far more water, and percolation down and outward at the base explains the richer vegetation of inland dunes.

Table 2

Weather data for coastal and inland locales of the central Namib Desert. Temperatures are in degrees Celsius. Means in parentheses.

		Substrate temperatures			
		Surface		At 50 mm depth	
Location and month	Air at 2 m	Dune sand	Gravel	Dune sand	Gravel
1969					
Coastal	14,7–27,0	19,0–55,0	18,4–47,0	18,7–56,0	19,0–48,0
April	(19,1)	(30,0)	(24,5)	(33,4)	(26,8)
Inland	7,0–38,0	8,0–48,5	8,0–46,0	9,0–50,0	8,0–47,0
April	(25,5)	(31,5)	(25,6)	(28,5)	(27,2)
Coastal	6,0–35,0	8,0–35,0	8,5–33,0	8,0–35,0	9,0–33,0
June	(15,0)	(27,5)	(20,0)	(21,8)	(20,0)
Inland	4,0–35,0	6,0–38,5	5,5–36,5	6,6–43,0	6,3–42,0
June	(19,9)	(25,5)	(23,7)	(27,6)	(26,8)
Coastal	16,1–25,5	17,4–48,0	16,2–43,0	17,0–42,3	17,5–42,5
November	(19,9)	(33,1)	(30,3)	(34,3)	(31,3)
Inland	12,0–36,5	20,0–52,0	21,0–49,0	25,7–49,0	21,0–50,0
November	(24,4)	(37,3)	(30,6)	(36,7)	(32,7)
1970					
Coastal	16,8–34,0	19,9–67,0	19,7–45,0	20,3–70,0	19,5–45,0
February	(23,1)	(36,6)	(31,5)	(39,6)	(31,1)
Inland	10,3–42,5	14,0–83,0	14,0–80,0	14,0–85,0	14,0–83,0
February	(26,6)	(43,7)	(40,0)	(45,0)	(43,3)
x̄ Coastal	19,3	31,8	26,6	32,3	27,3
x̄ Inland	24,1	34,5	30,0	34,7	32,5

Data from personal records and the official records of the Namib Desert Research Station.

The daily fog regimen is well discussed by Logan (1960). Fog may be low or medium altitude, but drizzly ground fogs are frequent. Fog generally clears by mid-morning between 10:00 and 12:00 hours, returning by 15:00 hours, but varying with the time of the year, since in winter the sun is weaker and less vigorous in dissipating or preventing the return of fog. Indeed, some days the fog persists throughout. Another oddity is that maximum yearly temperatures along the coast coincide with the occurrence of the east wind in midwinter

(Logan 1960; Meigs 1966). In 1969 a June east wind gave a maximum of 33,9 C and in July 33,6 C, though winter 1969 was cooler and drier than normal. In January 1970 a midsummer maximum of 27 C was recorded, with no east wind condition. Logan considers east winds of rare occurrence. Winter minimums along the coast are to 6 C in June and July, about twice that in midsummer. Low maximum temperatures under fog were 11,4 C in July; 18,4 C in December; the corresponding lows for these days were 9,5 C and 14,5 C respectively, demonstrating the temperature insulating effect of fog. There is less temperature range in summer than in winter, though conditions do not vary greatly along the coast. The greatest temperature range is in winter with an east wind condition.

In summer, coastal winds are mostly northerly or north-westerly, often accompanied with drizzle when from the latter direction. Winter winds are southerly or south-westerly. Humidity is closely related to temperature, presence of fog and proximity to the Atlantic, being at or near 100% with low temperatures and fog. Near the coast humidity rarely falls below 90% even in the absence of fog cover. East winds drop humidity to 30%. Duration of fog and degree of humidity is less even a short distance from the coast, such as Swakopmund airport 1,8 km from the Atlantic, and lessens still further inland. Walvis Bay, partly protected by Pelican Point from the effect of the ocean, has conditions similar to Swakopmund airport and far less fog than at the Swakopmund lighthouse.

Fog has an effect at Gobabeb, but usually burns off sooner and returns later than along the coast. Air temperature minimums are lower and maximums higher at Gobabeb than at Swakopmund (Table 2). Though humidities of 100% occur, usually coinciding with fog, humidity tends to be lower at Gobabeb and as low as 5% with east winds. Other weather conditions are essentially as described for coastal sites, and are fully discussed for Gobabeb by Schulze (1969) and generally discussed by Logan (1960), Koch (1961) and Meigs (1966).

There is no great difference in dune sand and gravel substrate temperatures, other than for locality of both (Table 2). On dunes proper a considerable variation was apparent as to site and time of temperature data collected. For example, lee faces were hottest until such situations were shaded, when the crest was hottest. On winter afternoons dune lee faces are shaded earlier in the day. Dune temperature data have been omitted in this study, but Louw & Holm (1972) discuss these in detail in their study of the ecology of *Aporosaura anchietae*. Chamaeleons did not purposely seek cooler or warmer substrates or situations, as Warburg (1964) reported for vipers and Burrage (1966) for utas. Chamaeleons sometimes sought wind-protected sites to the lee of small objects. Burrage (1966) found a tremendous difference in thermal and textural qualities of nearby substrates and a consequent effect on the overall ecology of utas. Namib dune sand and gravel have an unfavourable heating gradient, barely heating under overcast conditions, when the substrate temperature approximated that of the air at 50 mm. Under clear skies dune sand and gravel heated rapidly to high levels, and cooled equally rapidly. Strong, sustained wind also depressed substrate surface temperatures. Because of this it is an advantage for *Chamaeleo namaquensis* that, thermally speaking, it is less dependent on the thermal qualities of the substrate than most reptiles. Schulze (1969) discusses the soil (gravel) thermal regimen at Gobabeb.

Logan (1960) and Koch (1961) give general consideration to Namib Desert flora, but Giess (1962, 1968) considers this in greater detail. Giess (1962) divided the Namib Desert flora into: (1) red dunes; (2) Kuiseb and Swakop Rivers; (3) Namib Flats north of the Kuiseb River stretching to the mountainous area of the Swakop Canyon and farther north from the Swakop River; (4) the mountains, such as Zwartbank, Vogelfelderberg, and isolated granitic koppies arising from the flats.

According to Giess (1968), coastal plants have a cushionlike shape due to wind and sand and assist in formation of small secondary dunes of varied height. Beach flora consists of *Psilocaulon salicornioides*, *Zygophyllum clavatum*, *Salsola aphylla* and occasional *S. nollothensis*. On the gravelly flats just inland of the strand are very scanty, widely scattered *Zygophyllum stapffii* and *Arthraeura leubnitziae*. Because of salt or gypsum, large tracts of these flats are barren. Eleven kilometres north of Swakopmund near Wlotzka's Baken great diorite boulders and stones shelter a richer flora, with *Drosanthemum paxianum*, *Ruschia*, *Tetragonia arbusuloides* and lichens. Sufficient rainfall permits growth of annuals. The gypsum plains have a rich growth of colourful lichens.

In dune regions the 'narras' (*Acanthosicyos horrida*) gives a thorny refuge to pursued reptiles. A few narras plants were found on the northern extremity of dunes at Swakopmund, though it is commoner on Gobabeb dunes. Large tufts of *Aristida sabulicola* are terribly overgrazed near the Kuiseb River in the Gobabeb area. *Aristida sabulicola* normally form hummocks on dune bases, the usually unharmed grass reaching heights of 1,5 m. *Acacia giraffae* trees occur on dunes near the banks of the Kuiseb River. *Tamarix austro-africana* (3–5 m high) are the commonest trees on the low dunes bordering the Swakop River. Both trees are frequently in various stages of burial by the shifting dunes. There are clumps of *Trianthema* sp. on small dunes.

The Kuiseb River has a distinct riverine forest, with large stands of *Acacia giraffae* and some *Acacia albida*. *Tamarix austro-africana* also occurs, but is virtually the only tree in the Swakop River region investigated. Density, variety and size of trees increase upstream. The exotic *Nicotiana glauca* is very common in the Kuiseb and Swakop River beds and bottomlands. *Salvadora persica* thickets line the banks of the Kuiseb River. Grasses consist of *Eragrostis spinosa*, singly or in thick stands, *Aristida sabulicola* (commoner in the Kuiseb River), and *Cynodon dactylon* and *Odyssea paucinervis* are found in damper spots. In the Swakop River *Trianthema* sp. occurs singly in clumps or forms low, broad-based hummocks, resembling hummocks formed by *Cynodon dactylon*. After floods and rains, a variety of annuals and especially pretty flowers appears in these areas.

The Namib Flats, or gravel plains, are practically devoid of vegetation along the coast and for approximately 12–18 km inland. About the only vegetation are sparsely scattered *Zygophyllum stapffii* (0,25–0,5 m high), and *Arthraerua leubnitziae*, occasionally forming small hummocks. *Zygophyllum stapffii* is the only large plant on the barren limestone outcrop on the north bank of the Swakop River. Aizoaceae occur in the watercourses along with *Z. stapffii*. Lichens are also present. *Welwitschia* occurs in this biotope. Farther inland appear shrubs such as *Sutera canescens*, *Citrullus eccirhosus*, the very small *Acacia reficiens*, *Asclepias filiformis*, and the larger *Parkinsonia africana*.

The mountains have a richer vegetation, especially of succulents, due to greater moisture from fog condensing on stones. Four succulents, one herbaceous Euphorbia, and an *Aloe* are recorded by Giess (1962). Lichens are also very abundant.

Mertens (1955) gives an excellent review of the reptilian co-inhabitants of *Chamaeleo namaquensis*. No information is available on the reptiles that directly compete with *C. namaquensis*, but the larger species of the lacertid genus *Meroles* do eat mainly tenebrionid beetles, which also form the bulk of the chamaeleon's diet. However, there is no information that either lizard eats exactly the same species of tenebrionids, and selection of different tenebrionid species by each lizard may not place them in too great a degree of competition with each other for this food. *Chamaeleo namaquensis* is the more ubiquitous saurian, while most *Meroles* species are restricted to sandy situations. Where *Meroles* and *Chamaeleo* co-inhabit, the lacertid is the more numerous. But greater population density of the lacertid does not necessarily mean it is the more successful saurian. The lower population density of the chamaeleon may be due to factors other than competition between these saurians. Furthermore, the population density of *C. namaquensis* does not greatly vary in all the diverse habitats in which it is found.

It seems that smaller reptiles chanced upon by *Chamaeleo namaquensis* are potential prey for it; the larger reptiles, potential predators of it. The only lizard that could prey on *C. namaquensis* is *Varanus*, which occasionally ventures from the Great Western Escarpment along the rivers into the barren desert. *Chamaeleo namaquensis* lives in the *Salvadora persica* thickets, which are also frequented by large cobras (*Naja*). *Bitis caudalis* may prey on *C. namaquensis*. Smaller snakes, saurians and sometimes geckos (*Rhoptropus*), are eaten by *C. namaquensis*. The nocturnal geckos, for example, *Ptenopus* and *Palmatogecko*, should be safe from *Chamaeleo namaquensis* because of their habits. *Palmatogecko* tracks were observed on the dune sand skirt of the limestone outcrop on the north bank of the Swakop River.

E. *Mortality*

1. *Parasitism and disease*

Elkan (1965) describes a fungal infection, probably by *Candida albicans*, destroying one half of the liver of a *Chamaeleo bitaeniatus*. Another *C. bitaeniatus* suffered a dermal fungal (Dematiaceae) infection. The reaction of the chamaeleon's skin was an increasing keratinization and thickening of the stratum germinativum, and ulceration of the dermis which contains the melanophores. This condition would prevent colour lability, disrupting chamaeleon thermoregulation and result in loss of appetite, general weakened condition and eventually death. An ailment affecting thermoregulation of *Chamaeleo namaquensis* and *C. pumilus* is discussed later under thermoregulation (see p. 55). It is not known what etiological agent was involved. These afflicted chamaeleons were unable to turn darker shades, and hence had trouble in warming at cool experimental temperatures. They had no difficulty in keeping cool at high experimental temperatures. Disruption of physiological thermoregulatory capacity greatly lowered the high metabolic rate of chamaeleons, resulting in loss of appetite, increasing listlessness, daytime sleeping, and eventual death.

Culex mosquitoes were observed feeding on *Chamaeleo namaquensis* at Gobabeb, South West Africa. Brygoo, Dodin & Sureau (1959) report *Culex fatigans* feeding on *Chamaeleo lateralis* and *C. verrucosus* of Madagascar. No other ectoparasites were observed on *Chamaeleo namaquensis* or *C. pumilus*. Brygoo and his associates have worked on the many protozoan parasites of Madagascan chamaeleons. Microscopic parasites were not examined in either *Chamaeleo pumilus* or *C. namaquensis*, but macroscopic endoparasites, which were encountered during autopsies of chamaeleons in association with investigations of diet, and reproduction, were removed. Dr Prudhoe of the British Museum (Natural History) kindly identified such parasites, and published his findings separately (Prudhoe & Harris 1971).

In January 100% of female *Chamaeleo pumilus* harboured intestinal parasites, but in October only 14,2% were so parasitised. In January, February, July and October 100% of male *C. pumilus* had intestinal parasites, but this incidence was only 16,7% in June. The greatest number of parasites was 70 nematodes removed from a female *C. pumilus*, whereas 36 was the largest number of nematodes removed from a male. In June a female *C. pumilus* weighin 15,4 g had a total parasite complement of 1,2 g consisting of 23 nematodes and 7 cysts variously on the bladder, ovaries and in the abdominal wall. It seemed healthy and yolking of follicles appeared normal. In April and August every *C. namaquensis* examined contained some parasites, but in June only 50% were parasitised. Intestinal parasites were mostly tapeworms in this species, with some nematodes, acanthocephalans and small cysts in the body wall.

According to Dr Prudhoe, the nematodes in *Chamaeleo pumilus* were all *Strongyluris*, but all the cysts were undergoing calcification, making them impossible to identify. However, one cyst showed great superficial resemblance to a cestode cysticerous. The cestodes of *C. namaquensis* were all *Oochoristica africana*, the nematodes *Physaloptera* sp., and the acanthocephalan larvae possibly of the genus *Echinopardalis*, which occurs as adults in mammalian carnivores. *Oochoristica africana* also occurs in the saurians *Agama* and *Meroles*. The cysts found in *Chamaeleo namaquensis* had also undergone calcification to a degree making accurate identification impossible. Helminths, covered by a gelatinous covering, were frequently observed among tenebrionid beetle remains in the stomachs of *C. namaquensis*. Chabaud & Brygoo (1960) and Brygoo (1963) record nematodes and trematodes of Madagascan chamaeleons, only the nematode *Strongyluris* being represented in their and this study's samples.

2. *Predation*

No actual field predation on *Chamaeleo pumilus* or *C. namaquensis* was observed. Defence is discussed later under that section in behaviour (see p. 73). While *C. pumilus* females are alleged (Rose 1950) to devour their young, this was found to be accidental, and triggered by a fruit-fly landing on or near the baby. Captured babies were not eaten, though usually killed by such mistaken identity on the part of the adults. A *C. dilepis* in captivity did eat young *C. pumilus*, and its presence caused some upset among the adults. Snakes of the genera *Dendroaspis*, *Dispholidus*, *Philothamnus* and *Thelotornis* are recorded (FitzSimons 1962) as predators on chamaeleons. According to Dr R. Jensen of Gobabeb, the raptorial birds *Falco rupicoloides*, *F. terinunculus* and *Melierax musicus*, and the mammal *Canis mesomelas*, prey on *Chamaeleo namaquensis*. Rose (1950) says shrikes eat *C. pumilus*, and, indeed, one can see the catch stored on barbed wire fences. Wager (1958) records cats, dogs, motor traffic, raptorial birds and snakes as mortality factors of *C. dilepis*, and also a spider ensnaring a young individual. Cats and dogs, particularly the former, preyed on *C. pumilus*, and the feral dogs of the Walvis Bay vicinity may prey on *C. namaquensis*. Chamaeleons sustained severe injuries, often fatal, as the result of intraspecific action (see under population structure, social interactions, p. 101).

3. *Physical*

Wager (1958) considers grassfires cause 'many thousands' of chamaeleon deaths. Fortunately, or unfortunately, none of the marked chamaeleon populations examined suffered any fires during the study period, so the real effect of this mortality factor cannot be estimated. Fire-ravaged grassy areas were combed, where previously *Chamaeleo pumilus* had been observed, but no remains were uncovered. *C. pumilus* at such sites appeared unscathed by such fires, provided they climbed high enough into tall reeds which were moist enough to resist burning, or evacuated to such nearby. It is not known whether chamaeleons found in burnt areas were simply returning refugees originally located there, or new individuals. Fire was scarcely a problem to *C. namaquensis*, since any burning of the meagre and scant vegetation of their habitat would be most local and easy to escape.

Fire is 'normal' in areas of scant or seasonal rainfall. Burrage (1966) feels that fire is beneficial to reptiles preferring open spaces, since fire clears dense growth that crowds such reptiles out. Fire would be beneficial to *Chamaeleo pumilus* in limiting tall trees from crowding out the bushes and grasses which it prefers, and which rapidly recover in burned areas.

No instance of flooding deaths in *Chamaeleo pumilus* is known, but any sudden, large increase in river volume would be suspected to have deadly effect on chamaeleons inhabiting stream-side vegetation. Flooding may be a mortality factor of those *C. namaquensis* directly inhabiting water courses in narrow canyons and bottom lands of intermittent rivers subject to sudden and erratic discharge. This would necessarily depend on the discharge at any given time of a given stream and the topography in the immediate area.

Burrage (1966) reports flooding of washes caused as high as 95% mortality of *Uta stansburiana hesperis* inhabiting such situations, though the effect on the overall population was minor. Those *U. s. hesperis* inhabiting a burn area of 2 050 m^2 suffered a 33,3% mortality.

Rand (1968) reports suffocation in nest-building *Iguana* of Panama, when their excavations collapsed and they could not free themselves. In captivity a male *Chamaeleo namaquensis* was rescued and survived a cave-in of its retreat burrow, but a female of this species died when its nest burrow collapsed.

4. *Human agency*

Setting of fires, spraying with insecticides, alteration of habitat, capture and killing for any of several reasons by man must rate as predation, since an animal permanently removed from a specific locality is denied to that local population as surely as if it had been killed and eaten. Alteration of the habitat is probably man's most destructive effort, because it totally eliminates a habitat and all forms dependent upon it. It was felt at Gobabeb that *Chamaeleo namaquensis* was rare there owing to the Kuiseb flooding in 1969. This is very much doubted. They were very much in evidence elsewhere along and in the Kuiseb away from Gobabeb, and flooding could not be a mortality factor on the gravel plains and dunes in the immediate Gobabeb area. Moreover, they were common in other riverbeds that were also subject to flooding at the same time as the Kuiseb.

Survival of *Chamaeleo pumilus* and *C. namaquensis* is discussed in the section on population structure (see p. 95).

F. *Temperatures and their control: activity patterns*

1. *Regulation of temperatures*

Most reptiles are considered ectotherms, though Benedict (1932), Templeton (1960), Dawson & Templeton (1963), Bartholomew & Tucker (1963), Norris (1967), Dawson (1967) and Weathers (1970) have shown that a number of forms supplement behavioural thermoregulation with purely physiological mechanisms. Ectotherms acquire and lose body heat by: (1) radiation; (2) conduction, primarily with the substrate; (3) air convection. Although at extremely high temperatures some lizards pant, this may be a wasteful recourse in the case of deserticulous species. Many diurnal forms maintain their body temperatures within narrow limits by behavioural adjustments, as demonstrated by Cowles & Bogert (1944).

Diurnal deserticulous lizards apparently have the most varied means of controlling their temperatures, employing physiological methods to increase their activity time beyond the restrictions of behavioural thermoregulation and in 'hostile' thermal conditions. This is discussed by Dawson (1967), Tucker (1967) and Mayhew (1968), who point out the following methods: (1) toleration of hyperthermia; (2) changes in surface-volume ratio by body expansion and contraction; (3) changes in reflectivity; (4) changes in the cardiovascular system affecting heat transport through the tissues. Richards (1970) discusses the use of evaporative cooling by reptiles.

2. *Thermal preferences in the field*

Chamaeleo pumilus is active even on rainy winter days that would seemingly deter any heliothermic reptile. It is able to be abroad because it is eurythermic and partly endothermic. Of 549 active *C. pumilus* body temperatures recorded, the overall yearly range was 3,5–37,0 C ($\bar{x}$ = 22,4 C; median 22,8 C). These data are given by season and weather condition in Table 17, and summarized in Table 3. Body temperatures differed according to season and weather conditions (Table 17). Seasonal differences have been reported in American iguanids by Tinkle (1967) for *Uta stansburiana* and McGinnis (1966) for *Sceloporus occidentalis*.

Fifteen records of low active body temperatures (3,5–9,9 C) for *Chamaeleo pumilus* were all taken under 'Cool Fair' conditions. Two *C. pumilus* with body temperatures of 3,5 C were catching flying prey. All these low readings,

Table 3

Environmental temperatures (°C) related to body temperatures (°C) and activity states of 603 *Chamaeleo pumilus* at Stellenbosch, Cape Province.

Environmental temperatures (Mean in parentheses)		Body temperatures	State and number of individuals			
			Basking Cool/Warm	Foraging Open/Shade		Retreat
32,0–39,0	(34,9)	36,0–37,9		4	6	
27,0–39,0	(32,7)	34,0–35,9		7	10	
27,0–35,0	(31,2)	32,0–33,9		17	15	
20,7–31,8	(28,3)	30,0–31,9		17	13	
19,0–32,5	(24,7)	28,0–29,9		27	4	
18,4–31,0	(21,7)	26,0–27,9	5	46	5	4
14,5–24,5	(20,0)	24,0–25,9	6	70	10	1
14,5–22,0	(18,8)	22,0–23,9	10	75	1	5
13,0–21,5	(17,1)	20,0–21,9	10	30		2
13,0–20,1	(17,8)	18,0–19,9	6	25	9	5
6,5–17,2	(14,5)	16,0–17,9	7	12	4	2
12,0–15,2	(13,8)	14,0–15,9	4	10		2
9,0–13,2	(11,6)	12,0–13,9	7	2		3
11,0–11,6	(11,3)	10,0–11,9	2	1		7
9,3–11,4	(10,6)	8,0– 9,9	2		4	6
5,0– 7,2	(6,1)	6,0– 7,9	5		3	3
3,6– 5,0	(4,5)	4,0– 5,9	1		5	5
2,0		2,0– 3,9		3		4
0,0– 1,7	(0,5)	0,0– 1,9				5

Numbers do not quite add up to 603, since some individuals were engaged in several activity states simultaneously.

however, were taken very early in the day (mostly before 08:00 hours), about 15 minutes before sunrise. These low body temperatures of active *C. pumilus* in the field agree with the body temperatures of 40,0 C recorded by Pearson (1954) for the Andean iguanid *Liolaemus multiformis*. Records for 45 *Chamaeleo pumilus* asleep and mostly taken at night range from 0,5 C ('Cool Fair') to 26,5 C ('Warm Fair'), and were almost the same as that of the air temperature at 50 mm (= Environmental Temperature). Body temperatures for active *C. pumilus* and for those at rest were monitored on a 24-hour basis. Table 6 gives a summary of body temperatures of selected lizards active in nature, which are co-inhabitants, or of similar habits as *C. pumilus* and *C. namaquensis*, the relevance of which is discussed later. These data are taken from Brattstrom (1965), though recent data have been included. Where the incorporation of new data differs from those of Brattstrom, the newer source has been credited.

Chamaeleo pumilus dies if held at −5,0 C for a minimum of two hours, and this temperature is considered the minimum lethal temperature. Though torpor does occur at this temperature, *pumilus* does react to pinching and prodding at 0,0 C and even −5,0 C for a time. The critical maximum temperature is 43,0 C; the maximum lethal temperature 43,0–47,0 C.

The body temperatures of active *Chamaeleo namaquensis* are remarkably stable, despite the varied environmental temperatures of the Namib Desert. On foggy mornings the substrate temperature was as low as 8,0 C; but on clear, sunny days the substrate temperature reached 67,0 C. Of 351 active *C. namaquensis* body temperatures recorded in the field, the overall range was 14,0–39,7 C; mean 28,7 C; median 28,8 C (Coastal, 14,0–36,2 C; $\bar{x} = 27{,}0$ C; median 28,4 C: Inland, 15,0–39,7 C; $\bar{x} = 30{,}3$ C; median 31,5 C). These data treated seasonally, are given in Table 17, and summarized in Tables 4 and 5. There is slight difference in weather and season in the means and between coastal and inland populations, but it is not significant. Though body temperatures of inland *C. namaquensis* were slightly higher, the range of body temperatures is about the same for the respective populations, regardless of weather conditions.

Most diurnal desert lizards have far higher mean body temperatures than *C. namaquensis* (Table 6) and this is discussed in the section on thermoregulation (see p. 37). *C. namaquensis* not only has the normal desertic problem of adaptation to and survival of high environmental temperatures, but also one of tolerating low environmental temperatures, or controlling its body temperature by physiological means. It solves its thermal needs to both environmental extremes by recourse to the latter solution. *C. namaquensis* shows discomfort at a body temperature of 41,0 C; is 'troubled' (seeks shade, mouth gaping, eye bulging) at 45,0 C; its critical thermal maximum was 47,0–48,0 C and lethal temperature was 49,5 C ±1,3. There was no difference in critical thermal maximum between inland and coastal individuals. The critical minimum temperature was 0,0 C for two hours; the minimum lethal temperature, −5,0 C for a minimum of two hours. Partial torpor occurred at a body temperature of 13,5 C (coastal), 15,5 C (inland), though pinching evoked response

Table 4

Environmental temperatures (°C) related to body temperatures (°C) and activity states of 272 coastal *Chamaeleo namaquensis* in South West Africa.

Environmental temperatures (Mean in parentheses)	Body temperatures	State and number of individuals Basking Cool/Warm	Foraging Open/Shade		Retreat
50,0–58,0 (55,0)	36,0–37,9	3	6		
67,0	34,0–35,9		1		
25,5–47,5 (36,0)	32,0–33,9	14	14		
20,5–45,0 (31,0)	30,0–31,9	20	10	6	
21,5–38,0 (25,5)	28,0–29,9	10	22	2	
18,2–47,0 (29,5)	26,0–27,9	29	33	6	
14,7–30,7 (21,4)	24,0–25,9	12	15	4	
20,4	22,0–23,9	10	16	8	
14,7–19,5 (17,1)	20,0–21,9	4	4	4	4
16,5–19,5 (18,0)	18,0–19,9	4	2	2	
14,0–17,0 (15,5)	16,0–17,9	2	2		2
8,0–16,0 (11,6)	14,0–15,9	4	4		6

Numbers do not add up to 272, since some individuals were engaged in several activity states simultaneously.

Table 5

Environmental temperatures (°C) related to body temperatures (°C) and activity states of 97 inland *Chamaeleo namaquensis* in South West Africa.

Environmental temperatures (Mean in parentheses)	Body temperature	State and number of individuals Basking Cool/Warm	Foraging Open/Shade		Retreat
48,5–58,0 (53,3)	38,0–39,9		5		
37,0–48,5 (41,5)	36,0–37,9		10	3	
34,0–40,0 (37,1)	34,0–35,9	4	8		
32,6–38,5 (35,6)	32,0–33,9		6		3
30,0–43,5 (40,7)	30,0–31,9	8	29		6
32,0–34,0 (33,3)	28,0–29,9				
30,0–36,0 (33,0)	26,0–27,9	4	8		
23,0	24,0–25,9	2			
—	22,0–23,9				
—	20,0–21,9				
—	18,0–19,9				
12,5	16,0–17,9	2			5
—	14,0–15,9				

Numbers do not quite add up to 97, since some individuals were engaged in several activity states simultaneously.

down to a body temperature of 10,0 C. Full torpor occurred at a body temperature of 7,6 C.

Field records (N = 18) of *C. namaquensis* at rest ranged from (coastal N = 11) 7,0–13,0 C ($\bar{x}$ = 10,6 C), and (inland N = 7) 9,0–16,0 C ($\bar{x}$ = 12,3 C) and were about that of the substrate.

3. *Thermal preferences in the laboratory*

In a laboratory thermal gradient active *Chamaeleo pumilus* body temperatures (N = 20) ranged from 7,0–30,0 C ($\bar{x}$ = 25,0 C), which is the ambient preferendum Von Frisch (1962) found. Bustard (1963) kept his *C. pumilus* at

30,6 C during the day. Laboratory resting temperatures (15,0–25,0 C; x̄ = 22,0 C) are similar to 'Warm Fair' field records, thus *C. pumilus* 'prefers' a higher resting (= nocturnal) environmental temperature, if it is available.

Like Von Frisch, Bustard (1965) did not take actual body temperatures, but records 36 captive *Chamaeleo hohnelii* active at an ambient temperature of 2,0–3,0 C and catching food at 10,0 C. Bustard (1966) also observes *C. bitaeniatus* is quite hardy, surviving ambient nocturnal temperatures of 36–39 F (2,0–4,0 C). Unlike *C. pumilus*, *bitaeniatus* and *hohnelii* of East Africa inhabit montane grasslands.

Chamaeleo namaquensis (N = 18) active preferred body temperatures ranged from 18,5–36,2 C (x̄ = 29,3 C), with no difference between inland or coastal individuals. The eccritic range was somewhat wider (14,0–39,7 C) but the mean (28,7 C) of both populations was close to laboratory findings. Stebbins (1961) gives a preferred body temperature range of 28,5–36,5 C (x̄ = 33,5 C) based on 27 records of two captive *C. namaquensis*. Greatest similarity in eccritic and preferred body temperatures is that for 'Warm Overcast' (coast 17,5–35,4 C; x̄ = 27,7 C: inland 20,0–39,0 C; x̄ = 29,0 C). The eccritic body temperatures of both populations do not differ considerably with most seasonal and weather conditions. Resting laboratory *C. namaquensis* body temperatures (25,0–29,7 C; x̄ = 28,7 C) were not really different from active preferred body temperatures, thus *C. namaquensis*, as *C. pumilus*, prefers warmer resting temperatures, if available. At night they did not select lower resting temperatures available, as Regal (1967) reported for some of his desert lizards.

As Mayhew (1968) points out, the eccritic and preferred body temperatures may be essentially the same for some species, but it is not the rule (Licht *et al.* 1966*a*, *b*). DeWitt (1963, 1967) found the deserticulous iguanid *Dipsosaurus dorsalis* to have a mean preferred body temperature of 38,5 C, whereas 42,1 C was the mean eccritic body temperature (Norris 1953). It is difficult to simulate in the laboratory the various weather conditions, such as rain, cloud, fog, and wind to which reptiles are subjected in the field. Thus, even if within the environmental range it is considered that laboratory thermal gradients do not give a clear reflection of the actual thermal factors of the environment, the thermal preferences of reptiles, or their need, ability, or lack of it to make thermoregulatory adjustments. This study agrees with Bustard (1967*b*), who thought that any difference in active preferred and eccritic body temperatures indicates that optimum temperatures exist for different functions. Artificially supplied temperatures also allow selection of, rather than regulation to, the preferred body temperature, without the variabilities imposed on it by other environmental factors.

4. *Thermal preferences of chamaeleons in comparison with other saurians*

The thermal preferences of co-inhabitants of, and species of similar habitat and habits as *Chamaeleo pumilus* and *C. namaquensis* are summarized in Table 6. Body temperatures of *C. pumilus* have a range similar to those of the Andean

Table 6

Summary of body temperatures (°C) of selected lizards active in nature, co-inhabitants of or of similar habits as *Chamaeleo pumilus* and *C. namaquensis.*

Species	Range	x̄	min. Crit.	max. Crit.	N	Ref.
Agamidae						
Agama atra	29,0–32,0	30,5			20	5
Amphibolurus barbatus	25,2–40,0	33,8			94	9
,, *caudicinctus*	34,8–41,0	39,0			15	9, 10
,, *inermis*	34,5–43,0	39,3			47	10
,, *reticulatus*	35,0–40,6	37,0			6	10
Physignathus longirostris	34,2–39,0	37,0			26	10
Moloch horridus	27,2–40,2	33,7			88	9, 14
Chamaeleonidae						
Chamaeleo dilepis	21,0–36,5	31,2			328	15
,, *namaquensis* (coast)	14,0–36,2	27,0			261	7
,, ,, (inland)	15,0–39,7	30,3	0,0	47,0–48,0	90	7
,, *pumilus*	3,5–37,0	22,4	−5,0	43,0	549	7
Gekkonidae						
Rhoptropus afer (coast)	19,0–38,0	28,0			550	5
,, ,, (inland)	28,5–36,5	32,7			12	4
Helodermatidae						
Heloderma suspectum	24,2–33,7	27,2			>57	
,, *horridum*	25,6–36,0	28,7			5	5
Iguanidae						
Anolis allisoni	28,2–36,6	33,0			122	
,, *allogus*	26,2–33,5	29,2			148	
,, *carolinensis*	18,0–37,5	27,0		41,8	25	5
,, *homolechis*	26,2–35,0	31,8			104	
,, *limifrons*	24,6–31,0	27,1			?61	1
,, *lucius*	24,8–32,4	29,3			86	
,, *sagrei*	27,4–36,1	33,1			178	
Basiliscus vittatus	22,5–38,5	35,0		41,0–44,6	720	
,, *plumifrons*	28,0–35,5	31,7			20	
Callisaurus draconoides	26,4–40,2	38,0	−3,0		>17	
Crotaphytus collaris	20,7–43,3	37,2	—2,0	46,5	>425	
,, *wislizeni*	23,0–41,4	38,3			>19	
Dipsosaurus dorsalis	27,0–47,0	40,0	0,0	47,5	many	
Holbrookia texana	32,0–40,2	37,1			6	
Iguana iguana	26,7–42,4	33,3		46,7	>37	
Liolaemus multiformis	4,0–37,0	35,0			?20	13
Phrynosoma coronatum	20,8–39,0	34,9	−3,0	46,7	>28	
,, *platyrhinos*	26,2–39,5	36,0		45,5	many	
,, *m'calli*	29,3–41,0	37,4			19	
Sator grandaevis	32,6–38,8	35,7			35	
Sauromalus obesus	23,8–42,0	37,9		45,6	many	
Sceloporus gracilis	30,3–39,1	33,6			38	
,, *graciosus*	20,8–38,2	34,2			101	
,, *jarrovi*	32,2–37,0	35,0			15	
,, *magister*	31,0–37,0	34,8	−3,0	43,0	many	
,, *merriami*	29,6–37,4	33,6			11	
,, *occidentalis*	26,4–38,0	35,0	−3,0	44,0–46,8	>500	
,, *orcutti*	26,0–38,5	35,4			21	
,, *poinsetti*	30,8–38,4	34,2			20	
,, *squamosus*	32,5–38,0	35,3			13	
,, *undulatus*	25,0–38,9	34,8		43,7	>54	
,, *variablis*	33,1–40,0	34,1		43,0	110	
,, *woodi*	32,0–39,2	36,2		44,2	42	

Table 6 *continued*

Species	Range	$\bar{x}$	min. Crit.	max. Crit.	N	Ref.
Uma notata	18,0–46,0	39,8			>529	12
,, *scoparia*	26,6–39,0	35,7			13	
Urosaurus auriculatus	32,3–39,0	36,3		43,5	25	
,, *clarionensis*	29,6–39,0	36,4		41,8	59	
,, *nigricaudus*	33,8–39,5	36,2			14	
,, *ornatus*	26,8–39,5	35,5		43,1	97	
Uta stansburiana hesperis	17,2–40,6	34,1			404	6
,, ,, *stejnegeri*	25,0–37,8	35,6			50	6
,, *thalassina*	32,6–38,8	35,6			22	
Lacertidae						
Aporosaura anchietae (coast)	26,0–42,0	34,0			100	5
,, ,, (inland)	26,4–38,3	32,4		45,1	13	4, 11
Eremias lineo-ocellata	35,0–41,5	38,4			16	
,, *namaquensis* (coast)	19,0–36,0	27,0			777	5
,, ,, (inland)	36,0–40,0	38,5			10	4
Meroles cuneirostris	24,2–39,1	35,0		45,4	24	4
,, *namaquensis*	36,0–40,0	38,5			10	
,, *reticulata* (coast)	19,0–36,0	27,0			852	5
,, ,, (inland)	25,0–43,0	38,6			111	5
,, *suborbitalis*	36,0–41,5	38,8		44,0	18	
Scincidae						
Eumeces fasciatus	13,5–37,0	33,0	−2,5		41	
,, *obsoletus*	17,5–36,3	34,0			39	
Lygosoma laterale	22,0–35,5	28,8			16	
Mabuya capensis	19,0–40,0	27,7			676	5
,, *occidentalis*	19,0–37,0	26,0			901	5
,, *striata*	31,0–39,5	35,8			121	
,, *multifasciata*	29,6–37,8	33,7			12	
,, *rudis*	25,4–38,6	32,8			31	
Sphenomorphus sabanus	24,0–28,4	25,8			16	
Tiliqua occipitalis	30,5–35,5	33,7			8	9
,, *rugosa*	25,0–41,0	34,6			125	9, 16
,, *scincoides*	29,5–39,5	34,9			9	2
Teiidae						
Ameiva ameiva	35,1–39 3	37,6		46,2	10	
,, *festiva*	32,0–39,8	36,2			70	
,, *quadrilineata*	24,0–42,0	37,6		45,1	698	
,, *pluvianota*	33,8–40,0	37,8			21	
Cnemidophorus ceralbensis	36,7–41,6	40,1			13	
,, *hyperythrus*	36,8–41,6	39,0			17	
,, *lemniscatus*	34,5–42,3	38,8			44	
,, *sexlineatus*	27,0–45,0	40,4			many	
,, *tigris*	29,0–44,6	40,4			>47	
Varanidae						
Varanus spp.*	20,0–40,0	36,0			12	3
,, *gouldii*	34,4–36,2	37,1			6	

* *acanthurus, gouldii, punctatus.*

Where uncredited, data shown are derived from Brattstrom (1965). Data for other species are identified by the following numbers to the references given below, as are the incorporation of new data for species listed by Brattstrom.

(1) Ballinger, R. E., K. R. Marion & O. J. Sexton (1970). (2) Bartholomew, G. A., V. A. Tucker & A. K. Lee (1965). (3) Bartholomew, G. A. & V. A. Tucker (1964). (4) Brain, C. K. (1962). (5) Burrage, B. R. (unpublished data). (6) Burrage, B. R. (1966). (7) this study. (8) Hirth, H. F. (1965). (9) Lee, A. K. & J. A. Badham (1963). (10) Licht, P., W. R. Dawson & V. H. Shoemaker (1966*a*). (11) Louw, G. N. & E. Holm (1972). (12) Mayhew, W. W. (1968). (13) Pearson, O. P. (1954). (14) Pianka, E. R. & H. D. Pianka (1970). (15) Stebbins, R. C. (1961). (16) Warburg, M. R. (1965).

iguanid *Liolaemus multiformis* and *Lacerta agilis* of the Russian Caucasian Mountains. *Lacerta agilis* maintains body temperatures 29,9 C above that of the environment (Strel'nikov 1944). Though their thermal problems are equivalent, the habitats of these three lizards are quite different, as *Liolaemus multiformis* and *Lacerta agilis* inhabit high mountains, while *Chamaeleo pumilus* does not encroach above lower mountain slopes. The montane chamaeleons, *C. bitaeniatus* and *hohnelii*, are 'active' in a similar thermal range in the laboratory, but for these species there are no field temperature data. These viviparous *Chamaeleo* may regulate to lower temperatures for reproductive reasons, which is discussed later in the section on reproduction. *C. pumilus* occurs sparsely in montane valleys and is subject there to lower environmental temperatures than those inhabiting lowlands.

The chief co-inhabitant of *C. pumilus* is the skink *Mabuya capensis*. *M. capensis* is active from 19,0–40,0 C ($\bar{x} = 27{,}7$ C), and is not abroad with body temperatures as low as *C. pumilus*, tolerates a body temperature slightly higher than the chamaeleon and has a higher mean body temperature. *Mabuya capensis* is rarely active in rainy weather, and usually keeps within dense vegetation avoiding exposure to the weather as does *Chamaeleo pumilus*. *Mabuya capensis* is chiefly a heliothermic skink, using dead vegetation as an insulator as does *Liolaemus multiformis* (Pearson 1954) and *Uta stansburiana* (Burrage 1966) to maintain very high body temperatures, much above that of the environment. How chamaeleons maintain higher or lower body temperatures compared to environmental temperatures is discussed in the thermoregulation—warming/cooling section (see p. 42). *Mabuya capensis* and *M. rudis* differ from most skinks in being active thermoregulators. *Agama atra* is another co-inhabitant of *Chamaeleo pumilus*. *Agama atra* is far commoner than the chamaeleon on mountain slopes; the reverse is true in lowlands. The agamids recorded ($N = 20$) had a body temperature range of 29,0–32,0 C ($\bar{x} = 30{,}5$ C).

The New World iguanid anoles (*Anolis*) are the ecological equivalents of the Old World chamaeleonids. *Chamaeleo pumilus* and *Anolis carolinensis* seem of quite similar habits and live under roughly comparable conditions. Most of the other species of *Anolis* listed in Table 6 are Neotropical, though some are mountain-dwelling, and others (e.g. *A. limifrons* and *A. frenatus*) inhabit closed canopy forests and are less warm-adapted than grassland or ecotone species, such as *A. auratus* and *A. tropidogaster* (Ballinger *et al.* 1970). Brattstrom's (1965) temperature data for *A. carolinensis* are for resting individuals, and those given in Table 6 are data collected by the author over several years from animals living in outdoor enclosures in New Jersey, Kansas and California. Thus, they are not 'field' body temperatures *per se*, but are all that are known of for this abundant species. The minimum voluntary body temperature (18,0 C) of active *Anolis carolinensis* is much higher than that of *Chamaeleo pumilus*, and the mean body temperature of *Anolis carolinensis* is slightly higher. However, the maximum voluntary body temperatures of both species are almost the same. *A. carolinensis* was also subject to approximately the same weather conditions, thus environmental temperatures are about the same, and judging the range of *A. carolinensis* (south-eastern United States of America) the similarity of these species seems valid. *Basiliscus* and some *Sceloporus* are also forms of somewhat similar habitat and habits as *Chamaeleo pumilus*.

Body temperature data of four *Chamaeleo dilepis* were recorded in the field at Windhoek, South West Africa. Data for this species are within the range Stebbins (1961) gives for 328 records of 30 captives. *Rhoptropus afer* is a co-inhabitant of *Chamaeleo namaquensis*. Like the chamaeleonid, there is a difference in the eccritic thermal preferenda of the coastal and inland populations of this diurnal gekkonid (Table 6). *Rhoptropus* only emerges when it can maintain a minimum body temperature of 19,0 C. It was never seen abroad during completely overcast conditions, but was active on the hottest days. At both times *Chamaeleo namaquensis* was active. *Rhoptropus* has temperature preferenda similar to the co-inhabitant lacertids *Eremias namaquensis*, *Meroles reticulata*, and the scincid *Mabuya occidentalis*. The principally dune-dwelling lacertid *Aporosaura anchietae* has been studied in detail by Louw & Holm (1972). This study's records are for coastal individuals only and appear to be slightly different from those of Brain (1962) and Louw & Holm (1972). *Aporosaura* is similar in psammophilous adaptations and thermal requirements to the iguanid genus *Uma* of the deserts of the south-western United States of America. Other desertic saurians are: *Cnemidophorus* (teiid), *Tiliqua* (scincid), *Callisaurus*, *Crotaphytus*, *Dipsosaurus*, *Holbrookia*, *Phrynosoma*, *Sator*, *Sauromalus*, (most listed) *Sceloporus*, *Urosaurus*, *Uta* (iguanids), *Heloderma* (helodermatid), *Amphibolurus* and *Moloch* (agamids).

Chamaeleo namaquensis has a low minimum voluntary body temperature for a diurnal desert saurian and most other species have far higher maximum voluntary and mean body temperatures. The American deserticulous iguanid *Dipsosaurus dorsalis* and *Chamaeleo namaquensis* are active in the extreme midday desert heat at environmental temperatures lethal to most birds, and probably all mammals. *Dipsosaurus* is active with a body temperature of 47,0 C on substrates reaching 60,0 C. A *Chamaeleo namaquensis* active with a body temperature of 34,2 C was recorded on vegetationless dune sand with a temperature of 67,0 C, and five records gave maximum voluntary body temperatures of 39,7 C for *C. namaquensis* on substrates with temperatures of 48,5–58,0 C ($\bar{x}$ = 53,3 C). Some of these chamaeleons were probably in transit between grass clumps, but others were in areas apparently devoid of any sort of available shade.

Gates (1970) contends that by knowing the properties of a particular species, one can predict the climate under which it must live. He has predicted the climatic parameters for *Dipsosaurus dorsalis*.

Iguanids, agamids and teiids are the most heat resistant lizards, skinks and xantusids are heat sensitive, while geckos vary in this regard according to species (Mayhew 1968). *Chamaeleo pumilus* is active over a broad span of body temperatures (34,5 C), but its critical minimum and critical maximum agree closely with such thermophilic deserticulous forms as *Callisaurus* and *Sceloporus* (iguanids), which are not as low as the heat sensitive skink, *Eumeces fasciatus. Chamaeleo namaquensis* has the same critical minimum and critical maximum as the iguanid *Dipsosaurus dorsalis. Chamaeleo namaquensis* cannot be described as thermophilic, but it is active over a narrower span of body temperatures (25,7 C) than *C. pumilus.* There are no other data on chamaeleon body temperatures in the field, so the thermal situation of *Chamaeleo pumilus* and *namaquensis* with other chamaeleonids cannot be discussed reasonably.

5. *Thermoregulation: warming/cooling in the field*

Chamaeleo pumilus and *C. namaquensis* thermoregulation is a complexly integrated process, involving dermal colour lability with attendant vasomotor and other cardiovascular adjustments, body posturing, thermo-pneumatic changes in lung and air sac volume, and panting.

Table 7 gives the skin colour and body compression indices referred to in this study. Body compression 'I' was the initial warming posture used by *C. namaquensis* and *C. pumilus* earliest and latest in the day, and occasionally during cool or unfavourable days to maintain body temperatures close to preferendum. It is also the resting position, being modified to initial warming by the chamaeleon assuming colour index '5' and positioning so that both sides of the body were usually in the sun, allowing the slanted rays of the rising or setting sun to strike the chamaeleon's body as directly as possible. Such a position gives the body a spherical shape and aids the warming of the upper part of the body, the lungs, air sacs, and probably the dorsal aorta. At this time the air sacs in *C. namaquensis* are inflated (Fig. 12B). In *C. namaquensis* this posture was coupled with thigmothermic behaviour. On chilly, foggy winter mornings coastal *C. namaquensis* experienced environmental temperatures of 8 C. The chamaeleons assumed body compression 'I' and colour index '5' and were closely adpressed to, but not ploughed into the substrate. The tail and legs were held close to the body. Such behaviour minimizes convective heat loss and thermoregulatory ploughing has no value, since temperatures warmer than that at the surface do not occur until a depth of 150 mm and greater. Under these weather conditions, the body temperatures and skin surface temperatures of the chamaeleons were no lower than 14,0 C. The substrate surface temperature directly beneath the animal is warmer by one or two degrees to that of exposed substrates. The animals remain still, moving out only for passing prey, territorial challenges, and courtship.

Under fair skies *C. namaquensis* ploughed thermoregulatory warming grooves in the substrate. In the mornings, such grooves were dug no deeper than 5 mm, but in late afternoons and evenings such grooves were ploughed to a depth of 15 mm. Digging deeper grooves later in the day allowed *C. namaquensis* to experience substrate temperatures a few degrees higher than that at the surface, whereas early in the day temperatures higher than that at the surface are only realized at depths of 150 mm and greater. However, a shallow groove early in the day minimizes convective heat loss, especially in the strong

Table 7

Colour and body compression indices for *Chamaeleo pumilus* and *C. namaquensis* in the field and in the laboratory studies.

Body Compression Index

	I	II	III	IV
Both species	body oval in cross section and adpressed to substrate with legs held to body	body cylindrical in cross section legs held away from and raising body from substrate	legs and body essentially as in 'II' but body slightly laterally compressed, especially dorsad; body width reduced 10% from that of 'II'	legs in stiff-legged stance directly under body; body an exaggeration of 'III'; extreme lateral compression; body width reduced by 30% from that of 'II'

Colour Index*

	0	1	2	3	4	5
*C. pumilus***	pallor	yellow	pale green	medium green	dark green	black
C. namaquensis	pallor, patternless white, light pink, gray, or sulphur yellow	ground colours dark pink, light gray, sulphur yellow, or light green; blotched or spotted pattern may occur	dark pink or yellow ground, with conspicuous spotted/mottled pattern and light to dark red brick dorsum blotches	dark gray or drab green ground colour; vitreous brick red blotches or white spots distinctly present	maroon, or dark, vitreous brick red ground colour, with distinct pattern	dark purple to black; usually uniform, pattern of white lateral spots indistinct if rarely present

* As that of Hogben (1924) (See also Zoond & Eyre 1934).

** Valid only for adults and juveniles with adult pattern. Other juveniles are either slate gray, light or dark brown, or black, thus are only '0' and '5', possibly '1'.

winds occurring under fair skies, and the slightly deeper grooves later in the day have the same value with the added benefit of a heat source. *C. namaquensis* periodically ploughed along uncovering more warmth as that at one site dissipated. *C. namaquensis* occasionally selected sheltered sites to the lee of dead vegetation, rocks, and other objects. The efficiency of initial heating within one hour is given in Table 8. *C. namaquensis* body temperatures increased by 9,5 C in the first 20 minutes after which heat uptake slows. Heating during the warmer season was somewhat faster, but the environmental temperatures were also higher.

Table 8

Efficiency of initial warming over the sixty minute period after sunrise (cool season only), in *Chamaeleo pumilus* (Cp) and *C. namaquensis* (Cn). Body compression ('CmI') and colour index ('ClI') are given in Table 7.

Temperatures (°C) increase Environmental	Body	N Species	ClI	CmI	Weather
8,0–10,0	14,0–25,0	6 Cn	5/5	I	fog, no wind
13,0–13,8	18,0–29,0	8 Cn	5/5	I	clear, strong wind
5,0–10,8	6,0–25,0	14 Cp	5/5	I	clear, light to moderate wind
13,0–14,5	12,0–20,0	10 Cp	5/5	I	rain, strong wind

Chamaeleo pumilus followed much the same mode as to body compression and colour indices as described above for *C. namaquensis*, except for use of substrates. Occasionally, *C. pumilus* would use metal objects (e.g. iron railings) acquiring some thigmothermic value as those selecting somewhat wind-protected sites. *C. pumilus* lacks air sacs, but the lungs are long, the distal parts of which might serve the same function as the air sacs in *C. namaquensis*. During warming and cooling thermoregulation, the lungs of *C. pumilus* and air sacs of *C. namaquensis* were brought to maximum volume, as can be deduced by the inflated appearance of the body in the field, palping, and verified surgically. The efficiency of *C. pumilus* when warming is given in Table 8. As in *C. namaquensis*, the fastest heat increase was in the earlier basking period, when *C. pumilus* body temperatures increased by 14 C in the first 15 minutes, the environmental temperature increasing only by one degree in the same period. Warmer season body temperature heating rates were as in *C. namaquensis*.

When initial warming has taken place, both chamaeleons switched to body compression 'IV'. In body compression 'IV' the body is greatly laterally compressed, reducing body width to 30% of normal, and the skin between the scales is greatly stretched. Usually only one side at colour index '4–5' was presented to the sun, the side in the shade being considerably lighter, usually at colour index '2'. Warming *C. namaquensis* at colour index '5' and body compression 'IV' with the skin thus stretched, have some of the scales edged in, and small flecks of the skin yellow and red. The whole body was positioned to receive the rays of the sun as directly as possible. The temperature of the side in the sun was read with a shielded probe and was at or slightly above that of the body; the side in the shade at, or a few degrees below. The chamaeleons periodically changed position, so that the side presented to the sun became the side in the shade and vice versa. The hue of each side changing during the turn around, so that the side facing the sun was always a darker colour, such as '4' or '5', and the side in the shade always lighter. They performed thus, even if the weather was overcast, presenting to the obscured sun.

Postural changes and assumption of different hues during the day varies somewhat with the environmental conditions, such as temperature, wind, cloud cover and rain. It must be noted here that chamaeleons in apparently identical situations were not necessarily the same colour, though body temperatures were about the same. Close observation revealed that the light phase ones assumed darker hues as their body temperatures dropped below the thermal preferential, and as their body temperatures rose their hues again lightened. In short, dark chamaeleons are raising their body temperatures to preferential. Chamaeleons at a colour index of '2–3' are at preferential. Fine adjustments included varying the side exposed to the sun. Efficiency of temperature maintenance is given in Table 9.

Table 17, showing thermoregulation through the seasons, veils important aspects by giving these data inclusively. For example, it amply shows the range of environmental and body temperatures per season for different weather conditions, but also implies that the higher body temperatures occurred with the higher environmental temperatures. This is not so, as most high body temperatures were recorded with lower environmental temperatures. This is brought out in Table 9, but *C. pumilus*, for example, 'Cool Fair', June 5, 11:00 hours, moderate south-west wind, environmental temperature (50 mm) 14,5 C; body temperatures (N = 5) 20,9–23,6 C ($\bar{x}$ = 22,5 C). This is also true of *C. namaquensis*; 'Cool Fair', April 14, 12N, calm, substrate temperature 55,5 C; body temperatures (N = 5) 30,0–36,2 C ($\bar{x}$ = 33,1 C).

Thermoneutrality occurs when the chamaeleon does not have to regulate to maintain thermal preferenda. This condition is realized with environmental temperatures of 23,0–26,0 C for *Chamaeleo pumilus* and 26,0–32,0 C for *C. namaquensis* under calm conditions. At such time they assumed a body compression of 'II', sometimes 'III', and skin colour of '3', and in some instances '2', which are the upper levels of the thermoneutrality zone. Dermal temperatures of both sides were about the same and close to the body temperatures. In *C. namaquensis* the air sacs were not in use, and in *C. pumilus* the lungs not filled to full volume. Also, the tail and legs were not held closely to the body.

As environmental temperatures soared, chamaeleons responded by reversion to body compression 'IV', rarely 'III', but never 'I' or 'II'. Colour was always '2' or lower, and the side to the sun lighter than the side in the shade. Complete pallor was assumed with a body temperature of 39,0 C for *C. pumilus*, and 30,0 C for *C. namaquensis* at abnormally high environmental temperatures. The lungs and air sacs filled and expelled air rapidly, and panting ensued. *C. namaquensis* was interesting in that occasional irregular panting with the

Table 9

Efficiency of body temperature maintenance in *Chamaeleo pumilus* (Cp) and *C. namaquensis* (Cn) selected to show extremes over the sixty minute midday period. See Table 7 for compression and colour indices.

Temperatures (°C)									
Environmental		Body		N	Colour index sides		Body compression		
Range	x̄	Range	x̄	Species	Sun	Shade	index	Weather	Season
14,7–15,0	(14,8)	20,0–25,0	(23,0)	10 Cn	5	5	IV	fog/drizzle, light to moderate wind	C
18,2–28,0	(23,1)	27,5–33,0	(30,0)	11 Cn	2–3	2–3	IV	clear, strong wind	O
16,0–16,5	(16,3)	20,0–23,5	(22,8)	19 Cp	5	5	I	rain, moderate to strong wind	O
17,0–20,8	(18,9)	22,8–30,8	(26,8)	14 Cp	2	2	IV	clear, strong wind	L
20,4–39,8	(30,1)	29,0–31,5	(30,3)	23 Cn	3–5	3–5	I	fog/drizzle, light to moderate wind	W
45,0–67,0	(56,0)	33,6–34,2	(33,9)	18 Cn	0–2	0–2	IV	clear, strong wind	A
26,6–39,0	(34,3)	30,0–35,0	(32,5)	15 Cp	1–2	1–2	I	clear, strong wind	R
20,0–27,0	(22,7)	26,0–34,8	(30,4)	15 Cp	3–5	3–5	I or IV	rain, moderate to strong wind	M

mouth barely open starts at a body temperature of 27,0–32,0 C, becomes periodic and regular at a body temperature of 36,0–37,0 C and continuous at a body temperature of 39,0 C, when the mouth is more widely open and the tongue gorged with blood and raised from the floor of the mouth. There was no preliminary panting in *C. pumilus*; juveniles began continuous panting with a body temperature of 33,1 C and adults at 37,0 C, with the mouth widely agape, the labial scales bulged outward, and the tongue much engorged with blood above the floor of the mouth.

Towards the end of the day, as solar insolation wanes and environmental temperatures drop, chamaeleons resort to darker hues ('4–5') and body compression 'I' and thigmothermic behaviour—including ploughing in *C. namaquensis*, and body compression 'IV' in *C. pumilus*. In short, the whole thermoregulatory process towards the end of the day is essentially a repeat of early morning warming. The loss of body temperatures over a period of one hour is given in Table 10.

Table 10

Fall of environmental and body temperatures of *Chamaeleo pumilus* (Cp) and *C. namaquensis* (Cn) over the one hour prior to sunset during the cool season.

N	Temperatures (°C) loss		
species	Environmental	Body	Weather
15 Cn	20,0–18,0	29,5–29,0	fog, light/variable wind to calm
19 Cn	35,0–24,0	29,0–27,0	clear, strong wind
17 Cp	16,0–13,0	23,0–21,0	rain, moderate wind
40 Cp	21,5–13,0	28,0–25,0	clear, light/variable wind

N.B.—Compression and colour indices for this time span are essentially as in Table 8.

6. *Thermoregulation*

Warming/cooling in the laboratory: Under artificial and natural conditions live chamaeleons heated faster than they cooled, while dead ones heated and cooled at the same rate. Table 11 shows *Chamaeleo namaquensis* and *C. pumilus* over a period of 300 minutes in total darkness and Table 12 in light. Equivalent results were obtained for a similar test with light and darkness alternated. It is apparent that skin colour liability does enable chamaeleons to raise and lower their body temperatures (Table 11). In the dark, no skin hue above colour index '2' was recorded. The rise of body temperatures was slow and it should be noted that both animals, though previously held at —5,0 C before the run, maintained body temperatures above —5,0 C. *C. namaquensis* body temperatures ranged from —2,0 to 1,9 C ($\bar{x}$ = 0,7 C); *C. pumilus* body temperatures ranged from —3,0 to —1,0 C ($\bar{x}$ = —2,5 C). Skin surface temperatures were equivalent in both animals throughout the experimental range. Body temperatures, especially those of *C. pumilus*, are considerably below the higher experimental temperatures.

Table 11

Body compression ('CmI' in roman numerals), colour changes ('ClI' in arabic numerals), and body temperatures of 10 *Chamaeleo pumilus* and 10 *C. namaquensis* in total darkness at various experimental temperatures (all temperatures degrees Celsius). See Table 7 for compression and colour indices.

Time from 0 in mins	Exptl temp.	*Chamaeleo namaquensis*						*Chamaeleo pumilus*					
				Skin temperature		Body temperature				Skin temperature		Body temperature	
		CmI	ClI	Range	Mean	Range	Mean	CmI	ClI	Range	Mean	Range	Mean
30	−5,0	I	0	−4,0 to −5,0	−4,6	−2,0 to 1,9	−0,1	I	0	−4,0 to −5,0	−4,6	−3,0 to −1,0	−2,5
60	5,4	I	2	3,1 to 3,9	3,6	2,4 to 2,7	2,5	I	0	3,5 to 4,0	3,7	3,5 to 4,7	4,5
90	8,6	I	1	6,0 to 7,5	6,8	5,5 to 6,8	5,9	I	2	7,0 to 8,5	7,6	7,0 to 8,0	7,3
120	11,9	I	2	10,3 to 10,9	10,6	9,4 to 12,0	11,1	I	1	10,3 to 10,8	10,6	10,6 to 12,0	11,2
150	13,8	I	2	13,2 to 14,0	13,8	13,1 to 14,1	13,6	I	1	13,6 to 14,2	13,8	13,0 to 14,1	13,4
180	14,6	IV	1	15,3 to 16,3	16,0	17,0	17,0	III	2	15,0 to 15,9	15,5	16,1 to 16,6	16,3
210	20,3	I	2	20,0 to 20,9	20,6	21,9 to 24,0	23,5	I	1	20,0 to 20,5	20,3	21,0 to 22,9	22,1
240	23,0	II	2	21,6 to 23,5	22,1	20,3 to 23,7	22,1	II	2	21,6 to 23,5	22,1	21,5 to 23,5	22,1
270	30,1	III	2	26,7 to 30,0	27,5	26,9 to 29,1	27,5	III	1	28,0 to 28,6	28,3	27,1 to 29,0	28,4
300	40,0	IV	1	28,0 to 29,9	28,6	29,9 to 31,1	30,0	III	2	26,5 to 29,9	27,4	28,8 to 30,8	29,4

Table 12 shows the results with these animals exposed to light. Active thermoregulation in *C. namaquensis* did not occur until the experimental temperature reached 5,0 C and was markedly so at 15,0 C; two degrees above voluntary torpor for this species. However, *C. pumilus* actively thermoregulated at the lowest experimental temperature. Dark phase (colour index '4–5') was evident on the light facing side of the animals at experimental temperatures, —4,5 to 25,0 C (*C. pumilus*) and 5,9 to 25,0 C (*C. namaquensis*). Thermoneutrality occurred in both species at experimental temperature 30,0 C, and cooling with light hues and less of body side presented to the light at experimental temperatures of 35,0 C and above. Body compression and panting were as in field observations.

Table 12

Body compression ('CmI' in roman numerals), colour changes ('ClI' in arabic numerals), and body temperatures of 10 *Chamaeleo pumilus* and 10 *C. namaquensis* in the light at various experimental temperatures. See Table 7 for compression and colour indices. Below, 'T' denotes time from 0 in minutes.

Chamaeleo namaquensis

	(°C)		Skin temperatures (°C)						Body temperatures	
	Exptl		Side to the light			Side to the dark			(°C)	
T	temp.	CmI	ClI	Range	Mean	ClI	Range	Mean	Range	Mean
30	—4,5	I	3	3,1– 3,3	3,3	1	1,2– 1,3	1,3	1,0– 1,9	1,7
60	2,5	I	3	4,8– 5,5	5,1	1	3,0	3,0	3,0– 4,4	3,9
90	5,8	I	4	7,8–10,0	9,1	2	6,9– 8,4	7,8	6,8– 8,5	8,1
120	15,0	IV	5	14,3–25,5	18,2	1	11,3–16,2	13,3	12,4–22,9	16,3
150	17,0	III	5	16,4–26,0	23,7	1	15,2–17,9	16,6	16,5–25,0	21,7
180	18,0	IV	5	21,1–27,6	26,2	1	19,0–20,5	20,2	20,3–26,9	24,9
210	25,0	III	4	27,5–33,5	31,6	2	24,0–25,0	24,6	27,5–32,0	30,8
240	30,0	III	2	28,4–33,3	31,3	1	26,5–31,0	27,7	26,2–32,6	29,4
270	35,0	IV	1	30,3–37,0	32,0	2	29,7–35,8	30,7	30,8–37,6	32,6
300	42,0	IV	0	35,0–36,0	35,6	2	33,0–34,9	34,3	34,7–35,7	35,2

Chamaeleo pumilus

	(°C)		Skin temperatures (°C)						Body temperatures	
	Exptl		Side to the light			Side to the dark			(°C)	
T	temp.	CmI	ClI	Range	Mean	ClI	Range	Mean	Range	Mean
30	—4,5	I	5	1,1– 1,2	1,2	2	—0,5– 0,0	—0,5	0,4– 0,6	0,6
60	2,5	I	5	3,5– 5,5	4,9	2	2,5– 4,0	3,3	3,5– 5,0	4,3
90	5,8	III	5	8,0– 9,0	8,5	2	6,3– 7,5	7,2	7,0– 9,0	8,5
120	15,0	IV	5	13,5–22,7	17,5	3	12,3–17,0	13,3	13,8–20,0	17,2
150	17,0	IV	4	15,1–23,5	22,0	2	14,5–17,0	16,0	17,0–22,0	20,5
180	18,0	IV	4	19,0–27,0	25,5	2	17,0–19,3	18,3	19,9–25,0	23,5
210	25,0	IV	4	27,6–29,5	28,2	2	23,0–24,0	27,0	27,0–28,0	27,4
240	30,0	IV	3	27,1–33,5	28,8	2	25,9–30,9	32,3	25,9–32,8	27,8
270	35,0	IV	1	31,2–34,8	32,3	1	31,0–33,2	31,7	31,0–35,0	32,3
300	42,0	IV	0	32,7–34,9	33,5	2	32,7–34,9	33,5	34,2–35,0	34,3

Table 13 shows thermoregulation of chamaeleons in an outdoor enclosure. These results were similar to those of field temperatures and need no further discussion.

Table 13

Effect of rising experimental temperatures in an outdoor enclosure on the thermoregulation of 10 *Chamaeleo namaquensis* and 10 *C. pumilus*, showing body compression ('CmI' in roman numerals), colour changes ('ClI' in arabic numerals), skin, and body temperatures. Air temperature at five centimetres (T_a 50 mm) is the experimental temperature for *C. pumilus*; and temperature of red Namib dune sand (T_s) is the experimental temperature for *C. namaquensis*. Below, 'T' denotes time in minutes. See Table 7 for compression and colour indices.

Chamaeleo namaquensis

	(°C) Exptl temp.		Skin temperatures (°C)						Body temperatures (°C)	
			Side to the light			Side to the dark				
T	T_s	CmI	ClI	Range	Mean	ClI	Range	Mean	Range	Mean
0	8,8	I	5	8,0– 9,5	8,8	1	9,3–11,0	10,0	8,5–10,5	9,6
30	16,5	IV	5	19,0–21,0	20,3	1	14,5–16,3	15,3	17,0–19,5	18,5
60	32,0	II	2	33,5–36,4	35,5	1	31,7–33,6	32,7	32,0–34,0	33,3
90	39,0	IV	1	32,5–36,0	34,5	2	33,0–35,5	34,0	36,0–39,5	38,6
120	50,0	IV	1	30,7–33,1	31,7	2	30,5–32,5	31,8	35,0–38,6	36,7
150	55,0	IV	0	24,5–28,0	25,7	1	23,5–27,0	25,3	33,5–38,0	35,7

Chamaeleo pumilus

	(°C) Exptl temp. T_a		Skin temperatures (°C)						Body temperatures (°C)	
			Side to the light			Side to the dark				
T	50 mm	CmI	ClI	Range	Mean	ClI	Range	Mean	Range	Mean
0	8,8	IV	5	7,7– 9,1	8,5	2	8,0– 9,5	8,5	8,5–10,3	9,3
30	15,0	IV	5	8,9–11,0	10,0	1	8,8–10,5	9,5	10,8–12,7	12,0
60	30,0	IV	3	18,5–20,5	19,7	2	18,0–19,5	19,0	23,5–26,0	25,3
90	35,0	IV	1	23,5–26,5	24,5	1	23,0–25,0	24,1	35,0–38,3	37,5
120	35,0	IV	1	22,0–24,9	22,7	2	21,5–23,5	22,5	32,0–36,0	34,3
150	37,0	IV	1	23,3–26,0	24,3	1	22,9–25,5	23,8	31,0–35,0	33,3

Comparing thermoregulation data collected in the field and laboratory it appears that the results are similar. But the slight discrepancy that occurs between field and laboratory are assignable to the fact that the animals in the laboratory tests were strapped so that they could not readily alternate body sides in presentation to the heat source, as demonstrated by the results of those in the outdoor enclosure which could alternate body sides and agree with the field data. This 'minor' variance seems important to the chamaeleons for fine thermoregulation. It must be noted that some chamaeleons never accepted being strapped down or in other ways adapting peaceably to the experimental process, regardless of the acclimation period.

7. *Cardiac rate and temperature*

The heart rate of *Chamaeleo pumilus* and *C. namaquensis* during heating and cooling was greater during rising body temperatures and lower during falling body temperatures at the same experimental temperature (Table 14). The values are similar to that Bartholomew *et al.* (1965) give for the scincid *Tiliqua scincoides*, and Bartholomew & Lasiewski (1965) give for the iguanid *Amblyrhynchus cristatus*. The elevation in chamaeleon heart rates at higher temperatures is assignable to the panic and frantic activity shown by both species at these levels. *C. pumilus* and *C. namaquensis* during cooling slightly elevated heart rates when their respective thermal preferenda were reacquired during cooling, as apparently does *Amblyrhynchus*. Again it must be noted that the cardiac rate of chamaeleons must be high, since no specimen adjusted to the test, nor was quiet during readings, their violent struggles being reflected. They seemed particularly irritated by the probe, which they made frantic efforts to dislodge. Therefore, except for the lower temperatures from 5 to 10 C, when *C. namaquensis* is torpid, the readings given are for very active animals.

Table 14

Heart rates of 5 *Chamaeleo pumilus* and 5 *C. namaquensis* in relation to heating and cooling at various temperatures.

Temp. °C	*C. namaquensis* Cooling	Heating	*C. pumilus* Cooling	Heating
	Heart Beats per Minute			
5	2,0	0,9	5,0	20,0
10	3,0	6,0	18,0	45,0
15	10,0	44,0	31,5	85,0
20	30,0	110,0	85,0	190,0
25	38,5	150,0	100,0	215,0
30	40,0	160,0	95,0	205,0
35	50,0	151,3	100,0	185,0
40	65,0	100,0	125,0	200,0
45	77,0	105,0	no record	

8. *Summation of chamaeleon thermoregulation in comparison with other reptiles; role of colour*

In summarizing and comparing chamaeleon thermoregulation with other reptiles, it should be noted that the known saurian usage of physiological temperature control methods are: (1) toleration of hyperthermia, which is non-existent in *Chamaeleo namaquensis* (maximum voluntary body temperature, 39,7 C), or *C. pumilus* (maximum voluntary body temperature, 37,0 C); (2) changes in surface-volume ratio by body contraction and expansion; (3) changes in reflectivity; (4) changes in the cardio-vascular system affecting heat transport through the tissues.

The ability of chamaeleons to change colour is the most noticeable integral part of chamaeleon thermoregulation. Aristotle (Crosswell's translation 1883) and Pliny (Bostock & Riley's translation 1887) first recorded that chamaeleons change colour, the former suspecting this to be a response to light and temperature. But it is an old fallacy that they do so to match their background, and such background-matching as does occur is the exception, not the rule, and quite incidental to the thermoregulatory function. It seems absurd that background-matching is so widely held—yet so easily disproved by direct observation. No studies have measured actual body and dermal temperatures at the varied hues, and their relationships to environmental temperatures or conditions.

This study has reported environmental temperatures and conditions, body temperatures and dermal temperatures at different hues in an integrated manner in the field and laboratory and in concert with other chamaeleonid thermoregulatory processes. From this it is concluded that colour change in *Chamaeleo pumilus* and *C. namaquensis* is primarily thermoregulatory, secondarily camouflage, and least important is background-matching.

Colour lability is a widely recorded phenomenon in invertebrates. The teleost fishes are the most proficient of colour labile vertebrates. For example, plaice can even match checkerboards and mosaics. Many reptiles, mostly the small desert saurians, have a wide range of colour change, and the agamid genus *Calotes* has probably the most versatile colour repertory. The young of some larger forms are colour labile, such as *Sauromalus obesus*, *Alligator mississipiensis*, and *Crocodylus niloticus*. There are pattern component changes in *Iguana iguana*. The tortoise *Chelodina longicollis* (Woolley 1956) is colour labile. The largest living lizards (Varanidae) are not colour labile, perhaps because they enjoy true endothermy by virtue of their size and proven physiological ability (Bartholomew & Tucker 1964). Rahn (1940, 1941) and Norris (1967) also discuss colour change in snakes of the genus *Crotalus* (Crotalidae), the deserticulous *Crotalus cerastes* being the most versatile at colour change.

The mechanics of chamaeleon colour change are mediated by expansion and contraction of melanophores in the first, innermost layer of the thick dermis. In expansion, the melanin extends into tentacle-like arms towards the surface through the other three dermal layers, which are: a uniform layer of white-reflecting cells; an irregularly distributed layer of blue-reflecting cells; an outer dermal layer composed mostly of xanthophores and a few erythrophores. The thin, transparent epidermis covers these dermal layers. The white-reflecting and blue-reflecting cells contain no pigment but intracellular-layered crystalline structures of guanine.

The blue- and white-reflecting cells do not function in colour change, but the xanthophores and erythrophores contract and expand, acting as a screen to give weaker or stronger effects. The blue-reflecting cells under the xanthophores give the typical green hue in a chamaeleon. The main effectors of chamaeleon colour change, the melanophores, disperse melanin into the cell arms which penetrate the other layers to mask one or more of them. Light green or yellow is mediated by melanin contracted below the white-reflecting layer, and the dispersal of melanin masking white reflection results in dark green. If melanin is dispersed over the xanthophores, the chamaeleon appears black.

Reptiles with the ability to change colour have the same complement of chromatophores as that described for chamaeleons, or some items missing, but all have melanophores, the chromatophores necessary for colour change.

Questions about colour change revolve largely around control of the colour mediating structures and secondarily the value to the animal of such change. It is not the purpose of this study to undertake detailed examination of the former, but an understanding of the latter is important as to how chamaeleons use colour change to maintain themselves in dynamic equilibrium with their environment.

Detailed studies on reptilian colour response, with valuable literature reviews in some, should be consulted in Atsatt (1939), Brücke (1852), Fuchs (1914), Hogben (1924), Hogben & Mirvish (1928*a*, *b*), Kleinholz (1938*a*, *b*, 1941), Krüger & Kern (1924), Longstaff & Poulton (1907), May (1924), Parker (1932, 1938, 1948), Rahn (1940, 1941), Redfield (1918), Sand (1935), Walls (1942), Weber (1881), Zoond & Bokenham (1935), Zoond & Eyre (1934), for early work, and Canella (1963), Coleman & Livezey (1968), Fingerman (1965), Hoesch (1961), Norris (1967), Talbot & Livezey (1964) and Waring (1963) for recent studies. Cleworth (unpublished data) is examining the electrophysiology of chamaeleon colour change by studies involving electron microscopy, skin reflectivity at dark and light adapted states, and light magnitude necessary to evoke change. Fingerman's (1965) and Waring's (1963) reviews provide excellent treatment of colour changes in all animals; the latter dealing only with vertebrates.

Colour change in reptiles is under nervous control in the chamaeleonids (Brücke 1852; Hogben & Mirvish 1928*a*, *b*; Zoond & Eyre 1934; Zoond & Bokenham 1935; Farghaly 1941), endocrine only in the iguanid *Anolis* (Kleinholz 1938*a*, *b*; May 1924), and dual in the iguanid *Phrynosoma* (Redfield 1918; Parker 1928). Part of the confusion of what mediates control is simply answered by different animals using different methods, as such would be expected in a polyphyletic group.

Canella (1963) questioned Hogben & Mirvish's (1928*a*, *b*) findings on chamaeleonids that epinephrine is not involved in excitement pallor, an error suggested by Parker (1938). Canella also found MSH, intermedin, ACTH, acetylcholine, pilocarpine, and atropine cause darkening. However, the presence of pigment concentrating nerves of the autonomic system in chamaeleons is still widely accepted. Perhaps complicating the picture still further is that all workers on chamaeleonids used species from different species groups (Farghaly: *Chamaeleo vulgaris* = *C. chamaeleon;* Canella: *C. jacksoni;* Zoond and co-workers: *Lophosaura pumila;* Hogben and Mirvish: *C. pumulus*, the latter two now synonymous with *C. pumilus*). The confusion of the identity of the last workers' subjects is reflected in Waring's (1963) review.

Cleworth (unpubl. data) has kindly summarized for me the results of his study on *Chamaeleo dilepis*, *C. zeylanica* (= *C. chamaeleon*), *C. pumilus* and *C. jacksoni*. Work on the last two species was discontinued, because the rough texture of their skin made reflection analyses difficult. Cleworth standardized ambient temperatures (22,0–25,0 C) to investigate effect of light on light- and dark-adapted animals. He found the skin of chamaeleons shows marked spectral sensitivity. Cleworth found that dark-adapted chamaeleons absorb heat, which is of considerable value at low temperatures. *C. pumilus* darkens to a greater degree than other chamaeleons. Heating effect of light-adapted chamaeleons is negligible, and is of reflective value at high temperatures. Regional differences in skin texture are not demonstrable, that is, the sides, the back and the belly are equally reflective. *C. pumilus* is not quite as reflective as *C. dilepis* (*C. namaquensis* would be more similar to *C. dilepis*), though this may not be owing to texture. Chamaeleons absorb a large percentage of incident light, especially at the near infra-red, with two main absorption peaks corresponding to those for water. More light passes through individuals with stretched skin, and all 'extra' transmission is through the inter-scale skin. Melanin acts as a 'flat black' substance over the whole spectral range (300–2 700 mμ). Cleworth observed migration of the allophore granules. Subcutaneous injection of MSH caused the injected area to go very black, giving an idea of maximal response. An area of illuminated skin can act independently, and response of the system to light is rapid, especially darkening.

Complicating studies of colour lability in *Chamaeleo namaquensis* are geographic variance of ground and colour pattern, which are discussed in the reproduction section. Hoesch (1961) gives an interesting account of the colours and patterns of this species. He found *C. namaquensis* is whitish gray at environmental temperatures up to 37,0 C, and that it becomes pallid at an environmental temperature of 40,0 C. Hoesch feels this is an adaptation to the desert in which it lives. He mentions the variation of black coloration covered with equidistant small white spots, and the variety of colour with pattern, which make assignment of colour indices a problem in this species. Hoesch also records a 'Schreckmuster' (fright muster) *C. namaquensis* assumes when confronted by a predator, for example a snake, *Bitis caudalis*. It is doubted that it is a fright muster, since *C. namaquensis* assumes it when suddenly sighting a food item (Fig. 8), or a mate (usually only females). Furthermore, an angry chamaeleon (see defence in section on behaviour, p. 73) assumes uniform black (colour index '5'). Thus, it is felt that colour index '5' is the fright or intimidation hue of angry *C. namaquensis*, as with *C. pumilus*, and this seems true of most chamaeleonids. Until further data are forthcoming, Hoesch's 'fright muster' is best considered an 'excitement pattern'. The speed of change ($<$1,6 secs) from uniform pallor completely to this excitement pattern and/or colour index '5' seems to indicate neutral control.

That chamaeleonid melanophores are served by pigment concentrating nerves of the autonomic system is generally accepted. The problem is do the nerves themselves mediate dispersal and contraction, is it humoral, or neurohumoral? Zoond & Eyre (1934) found nerve transection caused darkening of that part of the skin served by the severed nerve. Parker (1938) suggested that darkening of the skin area after nerve transection is due to excessive stimulation by 'injury currents', whereas Sand (1935) thought it due to lack of stimulation. That is, no nerve to carry the message equals no response, or darkening. It was frequently observed in wild and captive *Chamaeleo pumilus* and *C. namaquensis* that injuries inflicted in territorial conflicts were a perfect pallid outline of the attacker's teeth when the injured chamaeleon was dark (colour indices '4–5'), but the injuries were colour indices '4–5' when these same chamaeleons were lighter (colour indices '$<$2'). A large *C. namaquensis* attempting to eat a *Bitis peringueyi* was observed in the field. The viper bit the chamaeleon on the dorsum in the pelvic region. The fang punctures went black, surrounded by a small, pallid area. Within a week, these injury reactions normalized. Of further interest, an ailing *C. namaquensis* was injected intramuscularly in the tail, with 125 000 units of procaine penicillin and 0,12 g dihydrostreptomycin ('Strypen', May & Baker Co.). Ten minutes after the injection the left side of the head was black and the right side of the head was pallid, but the rest of the body was all black. Fifty minutes after the injection this chamaeleon was uniformly black. This might indicate that the antibiotic interfered with colour lability on an intracellular or enzymatic level.

Somewhat more drastic to the chamaeleons was the observation that before decapitation, all chamaeleons were uniformly black with rage, but upon beheading the body became instantly pallid while the severed head remained black. This reaction did not occur unless the spinal cord was cut, and would indicate CNS colour control of a high order of integration.

Ailing chamaeleons cannot readily change colour. The symptoms and some etiological agents are given in the section on parasitism and disease in mortality (see p. 31). Such affected chamaeleons were always pallid, and unable to effectively thermoregulate (Table 15). They were unable to warm as fast as normal chamaeleons who could assume colour index '5'. Diseased chamaeleons also cooled at a faster rate. At higher ambient temperatures the thermal relationships of sick and normal *C. namaquensis* seemed to be the same. Although some thermoregulatory aids still functioned, it was apparent that even they were less effective with an upset in thermo-colour-lability, and its attendant postural changes. Diseased chamaeleons were rarely other than body compression index 'I'. The skin temperature of such afflicted chamaeleons was that of the ambient air temperature. Also *C. namaquensis* with pneumonia seemed quite unable to warm or maintain heat. Unfortunately, all these data are for captives, though individuals in the wild would be more vulnerable to weather conditions and certainly to predation. Diseased chamaeleons eat sparingly, if at all, and their high metabolic rate dwindles. This indicates that colour lability is important in thermo-homeostasis of *C. namaquensis* and comparable data for *C. pumilus* are available.

Table 15

Thermoregulatory efficiency of diseased and healthy *Chamaeleo namaquensis*. Temperatures are in degrees Celsius. Means are shown in parentheses.

Time from 0 in mins	Exptl T_s	temps T_a 50 mm	Healthy (N = 7) Body temperatures Range	Diseased (N = 6) Body temperatures Range
30	10,0	10,0	9,5–12,0 (10,5)	7,5– 9,5 (8,5)
60	17,0	15,0	18,5–21,0 (20,0)	13,0–14,5 (13,7)
90	33,0	30,0	33,5–35,5 (34,3)	27,0–29,0 (28,0)
120	50,0	35,0	36,5–39,0 (37,5)	34,0–37,5 (36,0)
150	55,0	35,5	36,5–39,0 (37,5)	36,5–39,0 (37,5)
180	45,0	25,0	36,5–39,0 (37,5)	26,5–28,5 (27,5)

Longstaff & Poulton (1907) discuss the only protective value that colour may have for *C. pumilus*. Warming in the morning, a chamaeleon laterally compressed at body compression index 'IV' is black at colour index '5' on the side to the sun and light at colour index '2' on the opposite side, with the venter rather static at colour index '2'. This counterbalances the diminution of natural illumination from the open sky as the eye scans from the back to the sides to the venter on the animal, thus neutralizing shadow and conspicuousness. The light hue of the shade side neutralizes shadow, and the highly illuminated side presented to the light source is toned down by being dark, so the overall effect is to dissipate solidity. The ornamental knobs and crests disrupt the body outline melting the chamaeleon into its background. Such protective coloration may be most valuable to a chamaeleon warming during the cooler times of day, when assumption of dark (colour index '5') to the sun also has thermoregulatory value in absorbing warmth. Weber (1881) first proposed that dark coloration serves chamaeleons for warmth absorption and light for cooling. At hotter times of the day, assumption of a lighter hue facing the sun for cooling had less camouflage value depending where the *C. pumilus* was and it frequently selected sites which it did not match. The best overall matching were for chamaeleons on reeds surrounding vleis. The nocturnal resting hue (pallor) of *C. pumilus* made it quite conspicuous, and may be due to the old response of melanophores to contract in the dark.

It is generally regarded that chamaeleons cannot turn or acquire reddish hues, though erythrophores are in the dermis. On the reddish, interior Namib Desert dunes, most inhabitant *Chamaeleo namaquensis* have a pinkish or reddish ground colour with a pattern of brick-red blotches. On the grayish-white coastal dunes, most inhabitant *C. namaquensis* have a basic ground colour of sulphur yellow with a pattern of brownish or reddish blotches. But when warming, both inland and coastal phases of *C. namaquensis* assumed black (colour index '5') and on their respective substrates alone they were most conspicuous, especially on foggy mornings. However, where there were scattered debris on their highly contrasting substrates, the chamaeleons at colour index '5' appeared as artifacts and not readily noticeable. The colour variants of *C. namaquensis* are most difficult to see at colour indices of '<2' on their respective substrates.

Thus, reds, especially dark reds, may have the same thermoregulatory benefits of other dark colours, but a dark red chamaeleon in a green bush on a cold day would be noticeable and more vulnerable to predation. But a dark green chamaeleon on red or whitish-gray desert sand would also be conspicuous. Thus it is felt that red is beneficial for the Namib Desert dune-dwelling *Chamaeleo namaquensis*, just as a sulphur yellow or yellowish ground colour is concealing and valuable in thermoregulation for coastal Namib dune dwellers. Towards the better-watered and vegetated Great Western Escarpment at the eastern edge of the Namib, very dark greens appear in the inhabiting *C. namaquensis*. Thus, colour lability precludes habitat background-matching, since it is protective only at colour indices of '2–3' at thermoneutrality. The complexity of colours in *C. namaquensis* is furthered by the individual variety in base ground colour and patterns, which is discussed in reproduction under sex determination and description of adult *Chamaeleo pumilus* and *C. namaquensis* (see p. 109). However, an individual chamaeleon can only change from light to dark, as Farghaly (1941) and others have noted.

The importance of radiant energy to ecological studies was emphasized by Gates (1962). All radiant heat energy reaching the earth is divisible into visible spectrum 40%, infra-red 40% and ultra-violet and radio regions 20%. As Norris (1967) emphasizes, complicating the assessment of radiation impinging on reptiles are such environmental factors as cloud cover, fog, surrounding vegetation, substrates and local topography. Since the skin of a reptile is its 'first line' of defence or adaption to usage and/or protection from such extraterrestrial emanations, it seems logical that colour lability serves as this shielding regulator. Radiant energy penetrating an organism may be important to lizards with a pigmented peritoneum, which may be significant in infra-red absorption. Thus, as Bartholomew & Tucker (1963) observed, changes in dermal radiative properties may help in thermoregulation.

Detailed studies of dermal colour lability as it relates to saurian ecology have been made to date only on American desert lizards, principally iguanids. Atsatt (1939) pioneered this investigation and others have expanded it. These are given in the reviews of Norris (1967) and Mayhew (1968).

Atsatt (1939) observed blanching in *Uta* at 22,0–25,0 C, but the upper level temperature (30,0 C) used did not produce blanching in the thermophilic *Dipsosaurus* because it only emerges (dark hued) at a minimum body temperature of 33,0 C, but becomes pale after warming to a foraging minimum of 38,0 C. Atsatt found that except for some *Callisaurus*, which are first pale then dark, all iguanids at low body temperatures have dispersed melanin, whereas at high temperatures relative to normal activity levels they assume the light condition. Between the extremes, temperature is not an overriding influence, and illumination tends to regulate melanin dispersal. In this middle thermal range lizards tend to become dark when placed in light and vice versa.

The grasshopper *Kosciuscola tristis* is black at 15 C; at temperatures greater than 25,0 C it is a bright greenish-blue, and intermediate shades between 15 and 25 C. Paling occurs two to three hours after sunrise, darkening again in late afternoon. Colour lability of this orthopteran seems thermoregulatory to lessen the heating effect of the midday sun (Fingerman 1965). Thermal colour lability in other invertebrates, especially intertidal crustaceans, is also discussed by Fingerman, harmonizing with that given for vertebrates.

Virtually all amphibians and reptiles disperse melanin at low temperatures and concentrate it at high temperatures, agreeing with a thermoregulatory role. Rivalling any colour labile reptile, the anuran *Hyla versicolor* is dark at 3,0–5,0 C, and lightens with increased temperature. Deanin & Steggerda (1948) have shown that a pale *Hyla* reflects more light, principally the heat-producing longer wavelengths, than dark individuals. Cole (1943) demonstrated that dark-coloured reptiles more rapidly overheated than light-coloured ones.

Working with several reptiles, Krüger & Kern (1924) showed black in *Lacerta* serves for heat absorption and light filtering. Thus, quanta of light penetrating to the body cavity might harm tissues (this would be ultra-violet absorbed by DNA), but the skin effectively blocks this when melanin is dispersed. Hutchinson & Larimer (1960) confirmed Krüger & Kern's finding that melanin dispersed in the dermis blocks 80% of the radiation from penetrating the interior. Therefore, a warming lizard exposing itself to the sun can achieve warmth without harm. Mayhew (1968) reviews this problem of light penetrating the body cavity with pertinent references.

The role of the black abdominal peritoneum is often cited as the barrier to harmful light, but Hunsaker & Johnson (1959) found the outer skin the chief reflector of ultra-violet, mainly wavelengths of 187–310 mμ. Porter (1966) noted most earlier investigators used wavelengths atmospherically absorbed and not reaching the earth's surface. Therefore, he used wavelengths (290–2 600 mμ), comprising 97% of the solar energy reaching the earth. His results showed that the skin is the prime absorber of energy, followed by the muscles, and then by the black abdominal peritoneum. However, more ultra-violet than previously thought penetrates to the body cavity.

In *Chamaeleo namaquensis* there is a transparent abdominal peritoneum (Fig. 12), with black visceral peritoneum occurring on the digestive tract, save the stomach, and variously wholly, partly, or absent on the testes. Only the American deserticulous teiid *Cnemidophorus tigris* has a transparent abdominal peritoneum among other diurnal series, but this teiid is protected by a large, immobile deposit of melanin in the dermis. Warming *Chamaeleo namaquensis* would be protected from harm by a colour index of '5', but it is impossible to deduce how it protects itself when at the pale hues in the midday Namib Desert heat and high illumination, unless; 1) the transparent abdominal peritoneum has strong reflective capabilities (?); 2) the light phases of *Chamaeleo namaquensis* are more efficient in dermal reflectivity than has been previously recorded (Waring 1963; Norris 1967; Mayhew 1968). *Chamaeleo pumilus* has black abdominal and visceral peritoneum, which may wholly or partly cover the testes, rarely absent, and always shields the uterus. Mayhew (1968) notes that no lizard capable of marked colour change lacks a black abdominal peritoneum.

The previous discussion shows that warming reptiles expose themselves to light (=heat), and how they might protect themselves from the harmful effects of exposure to the sun; it reports dark phase (colour index '5') for warming *Chamaeleo pumilus* and *namaquensis*, light phase (colour indices '<2') for cooling individuals, and colour indices '2–3' for those at thermoneutrality. The same findings have been recorded for several American deserticulous iguanids, such as *Dipsosaurus*, *Holbrookia*, *Phrynosoma*, some *Sauromalus*, *Sceloporus*, *Uma*, and *Uta*, tropical *Anolis* (Ballinger *et al.* 1970), some gekkonids, several agamids, for example, *Amphibolurus* (Bartholomew & Tucker 1963), and *Moloch* (Pianka & Pianka 1970), and even snakes, for example, the deserticulous *Crotalus cerastes* (Norris 1967).

Norris (1967) computes the net energy gain at lightest phase (71,2 cal/min) and darkest phase (92,4 cal/min) for *Dipsosaurus*, a deserticulous iguanid roughly the same size as *Chamaeleo namaquensis*. Norris concludes that colour change has value as a heat flux control for warming *Dipsosaurus*. The same seems true for *C. namaquensis* and *C. pumilus* as well as *Dipsosaurus*. As Norris points out, the desert environmental temperature, coupled with local topographic conditions can put desert species in the centre of a reflector oven, where, he feels, colour lability would be of minimal value. Here other adaptations might be of importance.

It is doubtful that forced convection from wind is of importance to cooling in *Chamaeleo namaquensis*, since this species was often observed active without discomfort in wind-protected areas between dunes in sizeable pockets of still air (i.e. a reflector oven). Also, light is very bright in the Namib Desert, particularly in the coastal dunes, with high reflection from the substrate. The air temperature at two metres and the heat load in a reflector oven are stultifying and the light dazzling, yet *C. namaquensis* seems quite at ease, pallid to the sun, patterned to the reverse, and always at a body compression index of 'IV'. *C. namaquensis* has a white venter, which undoubtedly reflects light and heat rebounding from the substrate. The venter pattern of *C. namaquensis* and *C. pumilus* is similar, differing only in colour, and consists of a broad mid-ventral white or dusky-white band edged by a narrow, conspicuous band of light gray in *C. namaquensis*, greenish in *C. pumilus*, dorsal to which white resumes up to the main laterum colour. Reflection from the venter can be cancelled by adpression (compression index 'I') to the substrate. Although most reflectivity data answer problems of colour lability and thermoregulation for *C. pumilus* and *C. namaquensis*, the problems of a transparent abdominal peritoneum, and the reflective efficiency of the light phases of the latter yet remain. *C. namaquensis* inhabits areas devoid of vegetation, and rarely seeks relief in shade where shelter is present.

Some workers (Mayhew 1968) see colour as wholly, or chiefly for protective concealment (Schmidt-Nielsen & Dawson 1964). As Norris (1967) points out, best matching (see previous discussion p. 56) occurs at thermoneutrality. This is what Klauber (1939) was considering, actually predicting many findings made later, and he is not a proponent of colour being primarily for concealment. Norris (1967) and the author feel that if a dark-hued animal is not concealed while warming (cf. *Chamaeleo pumilus* and *C. namaquensis*), the rate of warming must be rapid (Table 8), so that thermoneutrality brings concealment coloration. *C. namaquensis* follows this, so it can be said that diurnal deserticulous species are generally conspicuous on pale habitats (cf. the permanently black Pisgah *Uta* reported by Norris 1967) when black during warming, but quickly gain concealment with paler hues at thermoneutrality and cooling. Thus, pale for thermoregulation and concealment are synergistic at high environmental temperatures.

Unfortunately, no data are available to compare *Chamaeleo pumilus* with non-desertic or 'temperate' colour labile forms, but it can be said that *C. pumilus*, subjected to prolonged cool environmental temperatures, is concealed best while warming at a colour index of '5' (reverse of desertic lizards) and at thermoneutrality, and quite conspicuous at the palest hues.

9. *Summation of chamaeleon thermoregulation in comparison with other reptiles; role of posture*

Body compression and associated colour lability in thermoregulating *Chamaeleo pumilus* and *C. namaquensis* are discussed in detail on pages 42–7. Body compression 'I' gives chamaeleons an ellipsoid shape in cross-section, increasing surface area by 30% and body width by 33,3%. The surface area of the back is especially increased, acquiring the outline of a large sphere. (See Norris (1967) for the value of this.) This posture, in adpression to the substrate minimizes convective heat loss, and concentrates initial warming on the mid-dorsum. Heating is exaggerated on the lungs of both chamaeleons and the air sacs of *C. namaquensis*, which lie close to the dorsum when inflated, and also on the dorsal aorta. The essentially body compression 'II' is considered the 'normal' body form and is a posture at thermoneutrality. The slightly laterally compressed body compression 'III' which only reduces body width by 10% is the other posture at thermoneutrality. Body compression 'IV' reduces body width by 30%, and increases the total surface area by at least 110%. Fine orientation increases or decreases the intensity of impinging insolation, such as the longitudinal axis presented with the head to the sun with the light striking on both sides of the chamaeleon's body; lateral body compression with the centre of one side directly facing the sun, or slanted so the sun obliquely hits that side. Frequently the chamaeleons tilted, so both sides received the sun, concentrated on the dorsum.

Body compression, mostly dorso-lateral flattening, has been recorded for various forms, for example, *Anolis* (Ballinger *et al.* 1970), *Amphibolurus*, *Sauromalus* and *Crotalus* (Norris 1967), and *Uta* (Burrage 1966). Heath (1962*a*) found that *Phrynosoma* facing into the sun achieves a more reduced heat load than when in the opposite position. Greatest heat load is when the lizard presents itself broadside to the sun.

Lillywhite (1970) demonstrated behavioural thermoregulation in the anuran *Rana catesbeiana*. By postural adjustments, this frog maintains active body temperatures of 26,0 to 33,0 C ($\bar{x}=30,0$ C), using pond water as a heat source or sink. Body temperatures of these frogs closely followed that of the dry bulb air temperature.

10. *Summation of chamaeleon thermoregulation in comparison with other reptiles; roles of the lungs, the cardiovascular system and temperature control centres*

Previously, lungs do not seem to have been considered as thermoregulatory aids in reptiles and information on this is circumstantial, since no probes were inserted into the lungs or air sacs of the chamaeleons. As stated, the air sacs of *Chamaeleo namaquensis* were pumped and held full during warming, and alternately filled and flushed in cooling. The distal parts of the lungs in *C. pumilus* acted as air sacs. Tornier (1904) made an exhaustive study on chamaeleon air sacs, including those located in the gular and occipital regions, which possibly aid in maintaining cranial thermo-homeostasis. Tornier showed that the air sacs are valved to regulate the passage of air, which is shunted in and held. He showed their value in puffing-up in defence, which this study endorses. However, the distal parts of the lungs of *C. pumilus* and *C. namaquensis* and the air sacs of the latter serve as dead air spaces, which when full and closely adpressed to the body wall could act as temperature stabilizers or reservoirs, maintaining even temperatures or insulation from high temperatures for the reproductive organs and other vitals to which they are closely adpressed (Fig. 12). Body compression increases the surface area of the lungs and air sacs. Couvreur & Gautier (1904) found a distinctly thermally correlated respiratory pattern in *C. chamaeleon.* involving flushing of the air sacs at 42,0 C.

Bakker (1971), in his paper on the probable physiology of dinosaurs and other archosaurians, postulates that chamaeleonids may use their lungs and air sacs in thermoregulation and/or for protecting their gonads. It seems that this suggestion is valid.

It could be assumed that chamaeleonids are not alone in using their lungs for thermoregulation, and that *Varanus* similarly uses its lungs. The lungs in *Varanus* are large, as in the chamaeleonids, and occupy a large part of the thoracic cavity, closely applied to the dorsal surface of the body cavity. When warming, *Varanus* flattens in the sun and laterally expands, increasing the surface area of the lungs. Since many reptiles do likewise, the role of the lungs in thermoregulation may be widespread.

The peculiar anatomy of the squamate heart (White 1959) and great vessels consists of a ventricle imperfectly divided into dorsal and ventral chambers. The ventricular base communicates with the atria, the right and left systemic arches and the pulmonary artery. The systemic arches join symmetrically, forming the dorsal aorta just posterior to the heart. The right systemic arch is the only supply to the head and anterior parts, other than a small connection from the left arch. This arrangement could favour a device for increased cardiac output for heat transport by allowing large volumes of venous blood to bypass pulmonary resistance. Concurrently, well-oxygenated blood could be supplied to the brain via the right systemic arch. Cardiac output could increase beyond the need for respiratory exchange without the energy expense to pass the whole cardiac output through the pulmonary circuit and without cutting the oxygen supply to the brain. The incomplete ventricular septum hypothetically could allow venous blood to exit directly via the left systemic arch and continue to the posterior parts of the body. Experimental data (White 1959; Tucker 1966; Baker & White 1970) have shown that the blood in the left systemic arch has an oxygen content equal to or somewhat less than that of the blood in the right systemic arch, but not vice versa, agreeing with the hypothesis that this arrangement could be of thermoregulatory value.

Thus, in warming, an open pulmonary circuit, with high systemic resistance, favours a cardiac left-right shunt, increasing the pulmonary blood supply for warming, with a well-oxygenated blood supply to the brain and major sense organs via the right systemic arch. When warming is completed the increase of pulmonary resistance would invoke a proper double circulation. Increase of this resistance would result in a systemic arch circulation, thus enabling the reptile to conserve heat through toleration of high anoxia in the posterior trunk. (See Gordon, Bartholomew, Grinnell, Jorgensen & White (1968) and Tucker (1967) for a discussion of reptile circulation, respiration and temperature control centres.)

An efficient peripheral vascular circulatory arrangement, involving shunts, is necessary for dermal heat absorption or reflection to have any importance in body temperatures. Cowles (1958) pointed to the importance of dermal temperature regulation in the development of endothermy. His elaborate experiments showed that lizards in fur coats benefited from insulation only when warmed. According to Cowles, in amphibians the vascularized dermis serves chiefly in respiration, but possibly the dermis also had a thermoregulatory function in extinct terrestrial labyrinthodonts. In reptiles the dermis serves in thermoregulation. In the truly endothermic birds and mammals the dermis functions in thermoregulation with fur or feathers for insulation.

Experimentally, Cowles (1958) demonstrated in *Dipsosaurus dorsalis* a temperature gradient is greatest during heat absorption; not so in cool air. Subdermally injected water blebs heated on one side only, showing that the heat is more rapidly dispersed on the radiated side, heat being transferred to the body interior in warming lizards. The dermal vascular supply was greater at higher warming temperatures. Trying Cowles's method with *Chamaeleo pumilus* and *C. namaquensis* yielded equivalent results, and at high temperatures the blebs were cooler on the radiated surface, indicating cooling. In cooling (pallid) chamaeleons, there was no gain in bleb temperature, indicating peripheral dermal vasomotor control, which may be mediated by the change of pigment dispersal itself. A lizard being cooled constricts peripheral circulation to preserve body core heat—as does one resting at night, and dilation of peripheral circulation upon basking allows a warmth exchange with the interior.

Bartholomew (1966), Bartholomew & Tucker (1963, 1964), Bartholomew, *et al.* (1965) and Weathers (1970) report representatives of the Agamidae, Iguanidae, Scincidae, Gekkonidae, and Varanidae heat faster than they cool. Some of these differences are attributable to endogenous heat production and circulatory adjustments. The degree of circulatory control of heat transport varies. In the agamid *Amphibolurus barbatus* 75% of the difference in heating and cooling is assignable to circulatory changes, but in the skink *Tiliqua scincoides* this difference is due to endogenous heat production. Varanids are intermediate. Much the same situation is seen in the marine iguanid *Ambly-*

rhynchus cristatus (Bartholomew & Lasiewski 1965). In the sea the cardiac rate drops and the peripheral vessels are constricted, with tolerance of anoxia in the body tissues, especially when diving. Basking on land, the peripheral vessels dilate as the cardiac rate increases. Thus, it should be emphasized that an increased cardiac rate and/or vascular bed adjustments are important in this process.

Heath (1962*a*, 1964*a*, *b*, 1965, 1966) has demonstrated differential head-body temperatures of as much as 3 C to 5 C in partly buried *Phrynosoma*, and De Witt (1963, 1967*a*) found this to be true also for *Dipsosaurus dorsalis*. Bruner (1907) describes sphincter muscles around the internal jugular veins. Contraction of these muscles reduces the flow of blood from the head. Closure of the internal jugular veins accompanies an increased heat flux from the head to the body in *Phrynosoma*, which Heath (1963) feels may be important in the thermoregulation of these lizards. Dissection revealed sinuses in the head of both *Chamaeleo pumilus* and *C. namaquensis*, but their functional significance was not investigated; they may possibly serve as in *Phrynosoma* and *Dipsosaurus*. Such a cranial circulation, as with peripheral circulation, would involve shunts.

Sensitivity of some centre is required to mediate reptile body temperatures to stability through use of the physiological methods discussed. Adams (1957) showed that chamaeleons possess a carotid body, very similar to that of mammals, which mediates blood pressure by increasing and decreasing stroke volume. The nature of the chamaeleon carotid body, the peculiarity of the chamaeleon lungs and air sacs, the nature of the squamate heart and great vessels, and the peripheral and cranial vascular supply would suggest a role of the cardiovascular system in thermoregulation.

Hammel, Caldwell & Abrams (1967) and Cabanac, Hammel & Hardy (1967) showed for the skink *Tiliqua scincoides* a thermally responsive (3 cold neurons, 5 warm—heat sensitive) region in the preoptic part of the brain. Heating or cooling the brain stem resulted in the appropriate behavioural thermoregulation for stabilization, but prematurely at higher or lower temperatures than normal. However, dermal and body temperatures also impinge on thermoregulation in this species. Saalfeld (1936) found similar thermal receptors in the medulla of lizards. Rodbard (1948), Rodbard, Sampson & Ferguson (1950) and Heath, Gasdor & Northcutt (1968) made similar findings for turtles.

This study records panting in *Chamaeleo pumilus* and *C. namaquensis*. Templeton (1960) showed for *Dipsosaurus dorsalis* and Dawson & Templeton (1963) for *Crotaphytus collaris* that panting dissipates 1,3 times the metabolic heat production at 44,0 C and felt the water loss negligible. *Chamaeleo pumilus* and *C. namaquensis* can easily maintain their water requirements, so this method of cooling could be most effective for them. Panting is recorded in several lizards (Dawson 1967; Mayhew 1968), except those that are not heat-resistant (e.g. *Eumeces obsoletus*), who pant weakly, or not at all, even under thermal stress. Varanids have a strong gular pumping action at high temperatures. Panting ensues close to the maximum voluntary body temperature, except in *Chamaeleo namaquensis* in which it begins early (see p. 47). Richards (1970), in a detailed review of panting, concludes that it is an ancient method, and true endothermy may have originated as a response to dissipating endogenous heat in hot environments.

11. *Oxygen consumption*

Table 16 shows oxygen consumption, breathing rate, and Q_{10} for *Chamaeleo pumilus* and *C. namaquensis* at rest and activity. Peak oxygen consumption was at 25 C for *C. pumilus* and at 35 C for *C. namaquensis*. The large increase in oxygen consumption for *C. pumilus* at 40 C was a reflection of the frenzied escape activities of the subjects at this temperature, and is so out of pattern and based on such few frantically active individuals that it might be advisable to ignore it. This seems odd, since *C. pumilus* was encountered in the field at environmental temperatures of nearly 40 C, but had a lower body temperature, perhaps assignable to the ease of thermoregulating in nature which they could not properly undertake in the oxygen consumption chamber. Except for those *C. pumilus* at 40 C, both species showed a reduction in oxygen consumption past their thermal preferendum. There was an apparent temperature difference in oxygen consumption between coastal and inland *C. namaquensis*, though they are reported here as a unit.

Literature reviews of the oxygen consumption of lizards are given by Dawson (1967), Tucker (1967) and Mayhew (1968). In the thermophilic *Cnemidophorus tigris* (teiid), and the less heat-resistant *Gerrhonotus multicarinatus* (anguid) and *Coleonyx variegatus* (eublepharid) the Q_{10} remains constant over at least 20 C, including low temperatures (Dawson 1967), but in the thermophilic iguanids *Crotaphytus collaris*, *Dipsosaurus dorsalis* and *Uma notata*, and the less heat-resistant xantusiid *Xantusia vigilis*, the Q_{10} varies with temperature, usually decreasing as the animals become warmer (Cook 1949; Dawson & Bartholomew 1958; Dawson & Templeton 1963). The equivalent-sized *Dipsosaurus dorsalis* and *Crotaphytus collaris* have lower resting metabolic rates between 35–40 C than the less heat-resistant skink *Eumeces obsoletus* (Dawson 1960) and *Gerrhonotus multicarinatus* (Dawson & Templeton, unpublished data, see Dawson 1967), possibly because the first pair have lower oxygen requirements at high body temperatures. Below 15 C the heat-resistant forms show somewhat higher values than those that are less heat-resistant, indicating some cold sensitivity of the former.

Mayhew (1965) found in *Phrynosoma m'calli* (iguanid) oxygen consumption increased until 35 C, with a metabolic plateau at 35–40 C and a marked increase resumed at 45 C. He sometimes found quite a difference in oxygen consumption of laboratory and field measurements, though recorded under apparently indentical conditions. Bullock (1955) noted that such metabolic plateaus are not unusual. Schmidt-Nielsen, Crawford & Bentley (1966) record the iguanid *Sauromalus obesus* to have continuous oxygen consumption curves,

Table 16

Oxygen consumption, respiration rates, and Q^{10} of resting and active *Chamaeleo pumilus* (N = 15) and *C. namaquensis* (N = 15) at various temperatures. (Means are shown in parentheses.)

	Chamaeleo namaquensis			*Chamaeleo pumilus*		
		Active			Active	
Temp. °C	O_2 consumption $ml/O_2/gm/hr$** Range	Respirations per minute Range	Q^{10}	O_2 consumption $ml/O_2/gm/hr$** Range	Respirations per minute Range	Q^{10}
5	not active at 5 C		15–25 C	0,18–0,9 (0,41)	4–12 (8,2)	5–15 C
15	0,12–0,16 (0,15)	4–10 (7,0)	1,47	0,25–0,97 (0,53)	10–15 (12,5)	1,29
25	0,12–0,44 (0,22)	5–18 (10,8)	25–35 C	0,45–0,99 (0,67)	10–19 (15,3)	15–25 C
35	0,17–0,81 (0,64)	18–38 (26,1)	2,91	0,29–0,9 (0,55)	15–35 (25,5)	1,26
40	0,23–0,86 (0,57)	60–90 (85,0)	35–45 C	1,11–1,9 (1,31)	+100*	25–35 C
45	0,31–0,73 (0,42)	80–+100 (+90,0)*	0,64		no record	
		Rest			Rest	
5	0,02–0,06 (0,04)	0,03– 0,9 (0,3)	5–15 C	0,03–0,06 (0,05)	0,7– 2,0 (1,4)	5–15 C
15	0,03–0,09 (0,05)	0,1– 3,0 (1,1)	1,25	0,05–0,08 (0,06)	5,0– 7,0 (6,0)	1,2
25	0,03–0,09 (0,06)	0,7– 8,0 (4,0)	15–25 C	0,06–0,12 (0,10)	6,0–14,0 (7,0)	15–25 C
35	0,06–0,12 (0,10)	5,0– 9,0 (7,3)	1,2	0,08–0,13 (0,12)	6,0–11,0 (8,0)	1,67
40	0,06–0,14 (0,11)	20,0–24,0 (22,0)	25–35 C	no record		25–35 C
45	0,12–0,18 (0,17)	30,0–36,0 (33,0)	1,67	no record		
			35–45 C			
			1,7			

* Rate was too rapid for an accurate count.

** Corrected to standard temperature (0 C) and pressure (760 mm Hg).

but some had periodic peaks interrupted by periods of no detectable oxygen consumption, with a highly variable oxygen concentration of the air in the lungs.

Resting *Chamaeleo pumilus* showed a gradual increase in the Q_{10} of oxygen consumption values up to their thermal preferendum, but between 25–35 C the Q_{10} dropped to the same level (1,20) as that from 5–15 C. Resting *C. namaquensis* oxygen consumption Q_{10} values were variable, though generally increasing with temperature. The Q_{10} values of both these species of chamaeleons suggest they are in the less heat-resistant category of lizards.

In maximally active lizards Bartholomew & Tucker (1963) showed the Q_{10} of oxygen consumption in the agamid *Amphibolurus barbatus* to increase rapidly between 15–20 C, but to decrease thereafter. In *Varanus* spp. (Bartholomew & Tucker 1964) and the skink *Tiliqua scincoides* (Bartholomew *et al.* 1965) the maximal rates of oxygen consumption at various temperatures have a constant Q_{10} between 20–40 C, which are lower than the corresponding ones for resting animals. *Iguana iguana* between 15–30 C shows an active Q_{10} exceeding that for resting individuals. Active *Chamaeleo pumilus* had the greatest Q_{10} value (1,29) for oxygen consumption over 5–15 C, dropping slightly (1,26) over 15–25 C within the thermal preferendum of this species, thereafter dropping sharply. Oxygen consumption of active *C. namaquensis* had a Q_{10} of 1,47 between 15–25 C, with the greatest Q_{10} value (2,91) between 25–35 C within the thermal preferendum of this species, dropping very sharply (0,64) thereafter. *C. pumilus* and *C. namaquensis* active Q_{10} values were greater than those for resting individuals, except for the respective values at 25–35 C (*C. pumilus*) and 35–45 C (*C. namaquensis*) when the reverse was true.

Measurements of metabolic rates of maximally active and resting lizards may indicate the available energy to them for activity at various temperatures ('scope for activity' of Fry 1947). Moberly (1964) notes that this is complicated by indications that these animals rely extensively on anaerobic metabolism during activity, so oxygen consumption measurements may not give the full extent of energy utilization. Schmidt-Nielsen, Crawford & Bentley (1966) report continuous oxygen curves for *Sauromalus obesus* (iguanid), but other curves had periodic peaks interspersed with periods when no oxygen consumption was detectable. The same phenomenon was observed in *C. pumilus* and *C. namaquensis*. Aerobic scope for activity is maximal at 20 C for *Amphibolurus barbatus*, approximately 15 C below the activity temperature and thermal preferendum of this species. *Iguana iguana* has its maximum aerobic scope for activity at about 31 C; five degrees below its activity temperature. But in *Varanus* spp. with activity temperatures between 35,5–37,1 C and *Tiliqua scincoides* with an activity temperature of 32,6 C, the aerobic scope for activity increases with temperature between 20–40 C.

Without comparative data for other chamaeleonids, generalizations of data for *Chamaeleo pumilus* and *C. namaquensis* to that for other lizards have little meaning. All lizards discussed in the above paragraph were stimulated to maximal activity by electric shocks. Since chamaeleons struggled ceaselessly, electric shocks seemed unnecessary. *C. pumilus* appeared, however, to follow the pattern of *Amphibolurus barbatus*, whereas the greatest aerobic scope for activity of *Chamaeleo namaquensis* was at its thermal preferendum, which may corroborate its ability to stabilize its body temperature by the physiological methods discussed elsewhere. The slightly higher Q_{10} of *C. pumilus* between 5–15 C indicates its ability to be active at low temperatures.

Water loss in respiration is discussed in the section on 'Water and salt balance', and further remarks on metabolism are given in the section on 'Food habits'.

12. *Activity patterns: daily and seasonal*

Chamaeleo pumilus and *C. namaquensis* emerged from overnight spots independent of weather in all seasons. To be sure, prolonged days of rain discouraged *C. pumilus* activity in the open, but it was active within dense vegetation, which afforded shelter from heavy, driving rain, and probably more importantly from strong accompanying winds. Soft rain and occasional intermittent showers had no marked effect on discouraging activity in the open. In fair, or cloudy weather *C. pumilus* spent the night in exposed conditions, so that the first rays of the rising sun struck them early. Thus, *C. pumilus* was active as early as one hour before sunrise. This was particularly true of 'Fair Warm' days, though it must be remembered that the environmental temperature (T_a50 mm) was often quite warm. A daily minimum in summer of 11,5 C (T_a2 m) was recorded, and a summer minimum as low as 6,0 C has been officially recorded.

The daily temperature regimens of *C. pumilus* are given in Table 17. Cloud cover of 30% or more was considered overcast, since at that minimum coverage alteration of environmental temperatures was noted. Inspection of the data for 'Cool Cloud' and 'Cool Rain' show chamaeleon body temperatures to be higher than environmental temperatures. And as previously emphasized, high chamaeleon body temperatures were not necessarily recorded with high environmental temperatures. Details of heat maintenance are given in the thermoregulation: warming/cooling section (pp. 42–7). Excessive heat was not a problem for *C. pumilus*, since it mitigated this by resorting to shade.

C. pumilus retired for the night at paler hues and with body temperatures higher than those at emergence. This was about the same time as sunset. Retiring with paler hues may be an effect of insufficient light intensity to excite melanin dispersal, as Cleworth's (unpublished data) experiments indicate. Dermal heat exchange is reduced by a lower heart beat and peripheral vasoconstriction would conserve body core heat by reducing the blood flow to the periphery.

Chamaeleo namaquensis spent the night in various shelters, such as burrows, rock crevices, in thick vegetation, and sometimes in the open. Those not in burrows always ended their daily activity in the shade away from the setting sun to the lee of some object. This strange behaviour proved as 'correct' as

C. pumilus settling down in exposed sites, since both methods afforded access to the first rays of the rising sun on the following morning. The previous remarks for *C. pumilus* upon retiring are also applicable to *C. namaquensis*, except of a night when the latter goes into a full torpor from which it was very difficult to arouse.

Body temperature data for *Chamaeleo namaquensis* are in Table 17. Overcast criteria are as for *C. pumilus*. But it should be noted that fog was the usual overcast type for *C. namaquensis*, especially coastal populations, for which no distinction is made for drizzle, the rare event of rain, or whether the fog was down to the ground or at what altitude.

Of note was the stability and often narrow range of *C. namaquensis* body temperatures after initial warming, as compared to that of the environmental temperatures, regardless of the population considered. Highest and lowest environmental temperatures were recorded at the coast.

There is no inland record for 'Cool Overcast'. The substrate in 'Cool' months heats almost to as great (48,5 C) a maximum as it does in 'Warm' months (58,0 C), though the corresponding maximum body temperature records at these readings were 39,7 C ('Cool'), and 37,0 C ('Warm'). 'Warm Overcast' has maximum environmental temperatures eight degrees cooler than 'Warm Fair'.

Coastal populations were subjected to more varied environmental temperatures than those recorded at inland locales. Coastal 'Cool Overcast' environmental temperatures were as low as 8,0 C, and the coastal 'Warm Fair' maximum environmental temperature was 67,0 C. The body temperatures of active *C. namaquensis*, subject to these environmental temperatures, were 14,0 C and 34,2 C, respectively. For 'Partly Cloudy' conditions, the clearing of the fog was reflected in a sudden increase of the environmental temperatures, whereas the environmental temperatures drop upon the return of the fog. Of especial note with both *C. namaquensis* populations was the rapid increase in warming body temperatures in the early part of the day and the stability and narrow body temperature range independent of the environmental temperature throughout the bulk of the day. So, too, towards the end of the day body temperatures stabilized, even slightly rose, or declined very little in comparison with the rapidly dropping environmental temperature. Wind intensity has no effect on the activity of *C. namaquensis*. The thermal qualities of the surface of the substrate are discussed in the relevant section on habitats (pp. 28–9), and at depths in Table 45 in the discussion of incubation in the section on reproduction (see p. 115).

First daily order of business of *Chamaeleo pumilus* and *C. namaquensis* was basking (= warming), which upon their body temperatures reaching minimum operating levels (3,5 C *C. pumilus;* 14,0 C *C. namaquensis*), defecation, drinking, feeding and courting (see Behaviour, p. 72) usually followed. The previous arrangement is not meant to imply that this was the order followed, since neither chamaeleon was averse to forgoing drinking for a delectable prey item,

Table 17

Summary of environmental and body temperature (in degrees Celsius) relationships of 549 active *Chamaeleo pumilus* at Cape localities only, mostly Stellenbosch and vicinity, and 351 active *C. namaquensis* in the Namib Desert on the coast, mostly Swakopmund and vicinity, and inland, mostly Gobabeb and vicinity throughout the day in cool (April–September) and warm (October–March) months during daily weather conditions of; fair (0–29% cloud), rainy, overcast (30–100% cloud), and partly cloudy, referring to early morning and late afternoon fog in the coastal Namib.

				Body temperatures			Air temperatures 2 m			Environmental temperatures		
Locality	Season	Condition	N	Range	Mean	median	Range	Mean	median	Range	Mean	median
	C. pumilus											
Cape	cool	fair	97	3,5–30,1	19,9	22,5	2,0–30,1	18,3	17,9	2,0–30,1	17,0	17,9
,,	,,	overcast	84	11 0–29,8	20,6	21,0	4,0–27,0	15,6	16,0	4,0–27,5	16,3	15,5
,,	,,	rain	60	12,8–24,2	18,4	18,3	8,0–21,0	14,6	13,0	7,7–21,0	13,9	13,4
,,	warm	fair	137	17,0–37,0	28,1	28,5	15,0–42,0	25,4	24,5	15,0–39,0	25,2	25,0
,,	,,	overcast	88	14,0–30,0	24,3	26,0	13,3–29,5	20,4	19,5	13,0–29,0	20,0	19,0
,,	,,	rain	83	13,5–34,8	22,8	23,0	12,0–27,6	18,4	17,5	12,0–27,5	18,4	17,5
	C. namaquensis											
Inland	cool	fair	34	15,0–39,7	29,9	33,3	11,0–39,0	25,2	29,9	11,0–48,5	30,8	33,0
,,	warm	overcast	28	20,0–39,0	29,0	30,0	12,0–34,0	23,1	25,0	18,0–50,0	33,6	36,0
,,	,,	fair	28	26,0–37,9	32,0	31,5	16,0–38,0	27,2	30,2	26,0–58,0	41,0	41,0
Coastal	cool	overcast	31	14,0–29,0	21,9	22,0	9,0–17,0	13,2	12,8	8,0–28,0	18,4	18,3
,,	,,	partly cloudy	43	14,2–36,2	26,8	28,5	9,0–25,0	17,6	17,2	8,0–55,0	24,0	27,4
,,	,,	fair	51	14,5–31,0	27,3	28,3	9,0–27,0	14,4	14,6	8,0–47,0	21,3	22,3
,,	warm	overcast	39	17,5–35,4	27,7	27,8	13,0–22,0	18,1	18,0	14,2–33,9	23,5	26,5
,,	,,	partly cloudy	51	14,0–31,0	27,3	28,8	15,2–25,7	20,7	20,3	18,0–54,5	32,6	32,5
,,	,,	fair	45	23,4–34,2	30,9	31,1	18,0–25,5	21,1	21,0	18,0–67,0	38,4	40,6

N.B. See page 10 for environmental temperatures of *C. pumilus* and *C. namaquensis*.

an attractive mate, or repelling an invader. Also, some items are performed concurrently. *C. pumilus* frequently resorted to 'emergence' warming basking on cold or inclement days, though *C. namaquensis* rarely did so, even in drizzle and strong wind, though it did turn black (colour index '5') and assumed body compression index 'IV'. So, too, *C. namaquensis* (pallid to the sun, patterned on the side in the shade) was abroad during midday heat on the hottest days, though it would be hard put to find shade in such localities as the featureless gravel plains.

Chamaeleons appear to be wholly diurnal, as Uible (1968), Rosen (1950) and Spence (1966) report for those in the field, and Bustard (1965, 1966) and Von Frisch (1962) record for captives. In captivity chamaeleons kept pretty much to their wild regimen, but some captive *C. pumilus* and *C. namaquensis* were not averse to eating at night if illumination was provided. The exception was for captive females excavating nests, which is discussed further in the section on reproduction (p. 114).

Details of daily and seasonal activity for other diurnal saurians can be consulted in Mayhew (1968) for comparison with *Chamaeleo pumilus* and *C. namaquensis*. Excluding brumating species, as a rule seasonal changes include later daily emergence and earlier retreat in the cooler months, taking into account the effect of sunrise and sunset. Heath (1962*a*, *b*) records temperature-independent emergence in the iguanid *Phrynosoma*. Burrage (1966) found that different substrates have different thermal gradients and that this controls emergence in the iguanid *Uta stansburiana hesperis*, regardless of the weather. 'Normal' emergence, though, is about sunrise, or its equivalent. Ground fog has a delaying effect on uta emergence, but high thin fogs and no wind favour a 'greenhouse effect', aiding substrate heating. These emergent control factors are also noted in another iguanid, *Sceloporus orcutti* (Mayhew 1962), and the teiids *Cnemidophorus sexlineatus* (Fitch 1958; Hardy 1962), *C. sacki*, *C. perplexus*, *C. tessellatus* and *C. tigris* (Milstead 1957). The daily order of business and retreat time for most other saurians is as described for chamaeleons, but *Uta stansburiana* is active up to an hour after sunset (Irwin 1965; Burrage 1966) as is *Urosaurus* (Shaw 1950).

Midday increase in substrate temperatures and wind intensity are generally regarded as forcing saurians into retreats (Tinkle 1967, and Irwin 1965, for *Uta stansburiana stejnegeri;* Milstead 1957, for *Cnemidophorus perplexus*, *C. sacki*, *C. tessellatus* and *C. tigris;* and Bostic 1964, for *Cnemidophorus hyperythrus*). These factors do indeed have some correlation, especially for winds greater than 9,3 kph. But, as Burrage (1966) reports for *Uta stansburiana hesperis*, this may not be true on closer inspection, as utas are quite abundantly active under open vegetation, where the effect of wind is lessened and cooler substrates are found. Also, wind effect may be indirect, since utas restrict their activity to wind-protected sites because their prey are limited to such situations. Thus, the lizards go under open vegetation to find their prey in a concentrated and perhaps more vulnerable situation. *Chamaeleo pumilus* in intensifying wind sometimes restricted its activity to plant cover, because the flying insects which form its main prey were restricted to protecting vegetation by strong winds. *Chamaeleo namaquensis* was active in the strongest winds with blowing sand in the air and small gravel blown along the ground. Under such conditions, its prey was also abroad, even in winds strong enough to upset beetles and small lizards, such as *Eremias*.

G. *Behaviour*

1. *Senses*

Most studies of the senses of chamaeleons focus on their highly developed visual acuity, and it seems strange that the auditory organ should either not have developed (Hamilton 1960; Schmidt 1964) or degenerated (Miller 1966). While the auditory apparatus of chamaeleons is unique, the chamaeleonid cochlear duct could result from regression of the agamid type (Miller 1966). Only six of the 100-odd chamaeleon species have been studied: *Chamaeleo vulgaris* (= *C. chamaeleon*) by Versluys (1898) and Parker (1880); *Microsaura pumila* (= *C. pumilus*) by Parker (1880), Engelbrecht (1951) and Toerien (1963); *Lophosaura ventralis* (= *C. pumilus*) by Brock (1940); *Chamaeleo senegalensis* and *C. quilensis* by Wever (1968); *Brookesia marshallii* by Toerien (1963); *B. superciliaris* by Siebenrock (1893); *Rhampholeon platyceps* by Frank (1951) and Toerien (1963). The two common features of the auditory apparatus of those chamaeleons examined (see also detailed summary of Baird 1970) consists of: no tympanic membrane; fenestra ovalis very small, or absent. Other variations and details in the previously mentioned species can be had by consulting the preceding sources.

Anatomically, it appears that *Chamaeleo pumilus* would be deaf to air-borne sounds. Blindfolded individuals did not respond to the shaking of a pebble-filled can nearby, nor to a rock impacting on the ground. They did respond to something hitting a branch, but this could also be tactile. Wever (1968) showed that *C. senegalensis* and *C. quilensis* have a poor auditory sensitivity in comparison to other lizards, yet not far below that in many species with a conventional auditory apparatus. Wever (1968) found *C. senegalensis* and *C. quilensis* to have a frequency range extending from 100 to 10 000 cycles per second, with best sensitivity in the region of 200 to 600 cps. Blindfolded *C. namaquensis* were very alert to ground-borne sounds, as a rock dropped on sand, and particularly on a rocky or gravel surface. Shaking a pebble-filled can nearby caused them to turn and hiss in its direction.

The sight of chamaeleons is almost a legend in zoology. Excellent discussions of the chamaeleon eye and the host of pertinent literature are given by Johnson (1927), Walls (1942), Polyak (1957) and Underwood (1970). Polyak's account of vision in vertebrates is most valuable, noting the same chamaeleonid-type eye mobility and perhaps visual acuity in the American iguanid *Anolis carolinensis*, with binocular stereoscopy in this and several other forms. The more chamaeleonid-like *Chamaeleolis chamaeleontides* is an even more perfect duplicate (Wilson 1957). In *Anolis*, Polyak (1957) describes a 'sighting groove', a black area of decreasing width anteriorad, running from the anterior margin of the eye to the tip of the nose, which also occurs in esocid fish, among others. In the chamaeleonids this sighting groove is structural, rather than pigmented. It is widely stated in the literature that the chamaeleon eye is of 'unerring accuracy', and completely dependent on the functioning of both eyes. This study showed that nothing was further from the truth; especially in the latter instance.

Normal *Chamaeleo namaquensis* had an accuracy of 80 to 90% ($\bar{x}$ = 85,0%), but was usually a painstaking aimer, sighting at an object, positioning back and forth, and even taking sightings from different angles. *C. pumilus* and *C. namaquensis* often shot at moving prey, which conflicts with what Von Frisch (1962) notes for the former. Normal *C. pumilus* also tended to shoot with far less preliminaries and was accurate 75 to 92% ($\bar{x}$ = 86,0%) of the time. Discounting those temporarily blinded by the stings and bites of captured prey, several *C. pumilus* were found with only one functional eye. While the extent of this partial vision disability varied between individuals, some had one eye completely ripped out. These chamaeleons with only one functional eye had an accuracy of 57–63% ($\bar{x}$ = 60,0%). They aimed by fixing their sole eye on the target and slowly turned the head to face the target before shooting out their tongue. Adhesive tape on one eye was used to experimentally blind twelve each of *C. pumilus* and *C. namaquensis*; they were then allowed 24 hours' acclimatization. The chamaeleons were then given five daily trials at prey, all scoring zero on the first test day. By the close of the second day, the accuracy of both species was 15 to 30% ($\bar{x}$ = 22,7%), by the end of the third day, 45 to 55% ($\bar{x}$ = 50,1%), and by the end of the fourth day, 57 to 62% ($\bar{x}$ = 59,0%). They aimed in the previously described manner of naturally partly blind *C. pumilus*. If initially the left eye had been experimentally covered, there was no change in fourth day individual accuracy if the right eye was subsequently covered on the fifth day.

Of all squamates, Jacobson's organ is least developed in the chamaeleonids, and it may be reduced to a small pit without a mushroom body, as in *Microsaura pumila* (= *Chamaeleo pumilus*) (Malan 1946; Engelbrecht 1951), or absent in *Rhampholeon* (Frank 1951). Haas (1947) feels it is debatable as to whether Jacobson's organ has any sensory function in the chamaeleonids (Parsons 1970).

2. *Defence*

Chamaeleons habitually select a site as a retreat for the night, as is recorded for *Chamaeleo dilepis* (Wager 1958; Brain 1961), *Microsaurus pumilus* (= *C. pumilus*) of Von Frisch (1962), and *Microsaura damarana* (= *C. pumilus*) of Spence (1966), *Chamaeleo pardalis* (Bourgat 1968*b*), *C. jacksoni* (Bustard 1958), *C. hohnelii* (Bustard 1965) and *C. bitaeniatus* (Bustard 1966). In the case of arboreal forms, this is a favoured perch on a twig. While this was true of *C. pumilus*, in heavy rains it would climb to the underside of a large leaf and in its manner of gripping it, create a satisfactory umbrella.

Both sexes of *C. namaquensis*, in the field and in captivity, occasionally constructed burrows for retreats. While some were undoubtedly abandoned small rodent burrows, others were purposely dug by the chamaeleons. They were less elaborate than a nest burrow (see reproduction, p. 114). A retreat burrow constructed by a male 90 mm snout-vent, consisted of a terminal chamber 95 mm long, 63 mm wide, and 38 mm from the floor to the ceiling. The roof of the terminal chamber was 75 mm from the surface of the ground, and a narrow, gently sloping passage led 200 mm to the surface. Retreat burrows of *C. namaquensis* were usually located in some sort of a redoubt, as clumped vegetation, where the binding roots gave the soil greater cohesiveness, eliminating the danger of cave-ins. Those inhabiting rocky areas either used crevices and fissures in the rocks, or dug burrows in the gravel between rocks. Terentiev (1961) records fossorial habits of Saharan *Chamaeleon vulgaris* (= *Chamaeleo chamaeleon*). Similar burrows are dug by the European lacertid *Lacerta vivipara* (Burrage 1961), and by the American iguanid *Uta stansburiana hesperis* (Burrage 1966).

Camouflage value through colour lability in chamaeleons is synergistic with thermoregulation only at certain temperatures (see pp. 56–7, 59–60). Colour change in chamaeleons is primarily not for concealment, since when annoyed they become black, irrespective of background, and quite conspicuous. Thus, some colour lability in chamaeleons is emotional as the 'excitement pattern' of *Chamaeleo namaquensis* (p. 54). Schmidt & Inger (1965) note a normal *C. ituriensis* is forest green with large, irregular black spots, becoming dark if annoyed, but light green if victorious in combat (Bustard 1965, 1966, 1967*c*).

Upon the approach of a potential source of harm, *Chamaeleo pumilus* on a twig nearly always turned in an attempt to put the twig between itself and the object of its fear. The value of this is questionable, as in turning it flashes the longitudinally striped ventrum, which directs attention to its movement. Those that remained still were more difficult to detect. If annoyed, or faced with the further threat of harm, they frequently dropped and fell, as is described for *C. dilepis* (Brain 1961), or attempted escape in flight, without the wavering gait. *C. pumilus* did not feign death, as recorded for *C. dilepis* by Brain (1961).

C. namaquensis attempted escape in evasive flight, and could run very fast. However, if chanced upon when at rest, it kept perfectly still, except for the eyes, which rivet on its tormentor. There was no colour change, nor any reaction to having hands passed over them, or fingers straddling them. However, even if lightly touched, especially in the inguinal region, *C. namaquensis* exploded into challenge and fury. Leaping to a high, stiff-legged stance, it quickly became black, and inflated and laterally compressed the body. The throat was gorged, showing the yellow, reddish-orange interstitial skin, and the mouth held widely agape, accompanied to hissing (sounds like 'bissss'), and it often emitted a guttural growl (sounds like 'rrrr'). The mouth of adults has a yellow-orange interior, while that of the young is black. In this display, *C. namaquensis* turned and faced and frequently rushed its tormentor if further annoyed. Such action was usually quite startling and, in a moment of hesitation on the part of its antagonist, the chamaeleon changed to a lighter pattern and attempted to escape. It was most vicious when trapped, making repeated charges, and snapping its powerful jaws. While *C. pumilus* would bite if held, it was not painful, but a large *C. namaquensis* could inflict a powerful bite. *C. namaquensis* did not release its hold, but biting down hard, twisted and turned, and pushed and pulled in a most vicious manner.

3. *Learning ability*

Detailed studies of learning in reptiles are lacking, but some observations are warranted of evidence of learned behaviour, and modification of instinctive behavioural patterns in the light of past experience of the subject. *Lacerta agilis* (Rollinat 1934), *L. muralis* (Cooper 1958) and the iguanid *Uta stansburiana hesperis* (Burrage 1966) have been shown to demonstrate a Pavlovian response. Furthermore, when prey is in hiding, they attempt to flush it from cover by appropriate means.

Chamaeleo namaquensis and *C. pumilus* did not respond to Pavlovian sound stimuli, but would associate objects with food, as do the previously mentioned lizards. *C. namaquensis* would drink from the nozzle of a plastic squeeze bottle. During a food shortage several small males would accept dead food items such as large grasshoppers trimmed to size, and even devoured pieces of liver or meat. *C. pumilus* learnt to accept food from fingers, and both species quickly came regularly to food dishes, whether they contained a meal or not. Several *C. pumilus* often walked over to the enclosure containing the *C. namaquensis* to take the food of the larger species, successfully bluffing any which challenged them.

In hunting prey older chamaeleons demonstrated techniques which would be modified through experience and continually reinforced. Such instances were: (1) the safe overpowering of prey items capable of harming the chamaeleon; (2) the capture of prey which secretes itself during pursuit. The latter behavioural pattern was evidenced only by *Chamaeleo namaquensis* (see also food habits, p. 75). The chamaeleon would stop at the end of the prey's tracks and begin a careful search of the cover, beating small plants with its feet, or overturning small pebbles and other objects to flush the prey. If prey sought shelter in vegetation too large for the chamaeleon to trample, they lay in ambush until the potential meal emerged of its own accord within a reasonable period. Hatchlings would not do this, and by successive trials (15–25, $\bar{x} = 17$) of securing hidden prey, whether chased or not, the young *C. namaquensis* gradually seems to learn that out of sight prey was under cover.

Chamaeleo namaquensis and *C. pumilus* adults quickly recognized the potential harm that might be inflicted on them by such prey as large spiders, scorpions, hymenopterans, vipers and large lizards. Experienced saurian hunters disabled the capacity of such prey to inflict harm and seemed to know and recognized which part of the prey inflicted injury. In attacking such prey they adopted totally different tactics. First, they carefully viewed the prey, and then secured it so as to bring the teeth into play at once on that structure capable of causing harm, rather than a general, indiscriminate crushing. They then spat out the prey, viewed it again carefully and repeated the process until they were apparently 'satisfied' that no further danger existed. The prey was then taken in the normal manner. In the case of a large spider they aimed for the chelicerae; a scorpion, its terminal, poisonous sting; a wasp or bee, the most posterior part of its abdomen; a venomous snake or large lizard, its head. In the case of a very large scorpion, they disabled the large, clawed pedipalps after removing the sting. New-born young and hatchlings would not do this, and carelessly grabbed such items, often receiving a painful injury. They then wiped their head on the substrate and tried again. Within three days, all young handled such dangerous prey items as the adults.

The green anole (*Anolis carolinensis*) and another iguanid, *Uta stansburiana hesperis* also behaved similarly (Burrage 1966); seasoned hunters of both species being most cautious in attacking and disabling black widow spiders (*Latrodectes*), as though they fully realize the danger of this arachnid.

H. *Food habits*

1. *Feeding*

Chamaeleo pumilus stations itself on shrubs, grasses, reeds and wire fences in situations apt to be frequented by its prey, which it captures mostly by ambush. *C. namaquensis* regularly hunts, patrolling its territories, and securing any suitable prey chanced upon. The tongue only is used by *C. pumilus* and most often by *C. namaquensis* in catching prey. However, *C. namaquensis* often chased small lizards, beetles, and others attempting to escape it. *C. namaquensis* pursued those prey attempting escape, and when overtaking such prey on a parallel course, the chamaeleons simply snapped up the victim in their jaws in the normal saurian manner. They also lay in wait under plant cover and caught any suitable animal walking by, or beat and harried cover into which prey had sought refuge. Both species, but particularly *C. namaquensis*, meticulously masticate their prey before swallowing it, the tongue assisting. One forefoot was sometimes used to manipulate especially large prey.

Burrage (1966) reports that captive *Uta stansburiana hesperis* developed a taste for an egg mixture that was fed to alleviate insect shortages and served as a vehicle for medicine and nutriment for sickly specimens. Sick chamaeleons did not take to such fare and had to be force-fed.

Hotton (1955) gives an interesting and detailed account of the dentition of certain American iguanids, noting that lizard dentition is a reflection of the character of the integument and activity of the prey. In *Chamaeleo pumilus* there are usually 14 teeth in each half of the lower jaw, of which the first two teeth are the smallest, and teeth 6, 7, 11 and 12 are the largest. The teeth are all even and not tilted. The posterior teeth are broad-based, whereas the anterior teeth are conical. These teeth have faint anterior and posterior crenulations and the last teeth in the row have the central cusp pointing slightly backwards. Teeth 9–14 are set at an angle so that their bases are straight, but oblique to the jaw. There are usually 15 teeth in each half of the upper jaw, of which teeth 12–14 are the largest and tricuspid. The first three teeth are the smallest and conical. The posterior teeth have the main cusp tilted backwards very slightly. Only teeth 12–15 have slight anterior and posterior crenulations. Teeth 4–10 are very broad-based. In occlusion lower and upper jaw intermesh with each other.

In *C. namaquensis* there are usually 15 teeth in each half of the lower jaw, of which the first and fifth teeth are the smallest; teeth 6–10 and 15 are equi-sized; and teeth 11–14 are the largest. A line drawn through the crown apices is even in the anterior half of the jaw only, since the teeth of the posterior half tilt labially. Viewed from the side, the upper jaw is curved down at mid-point, so that the first and last teeth are at the same level, whereas those in between describe a gentle arc of 80°; the base of the tooth at mid-arc being equal in lateral line to the crowns of the first and last teeth in the jaw. In each half of the upper jaw, there are usually 16 teeth, of which teeth 12–15 are the largest, and from that point forwards they become progressively smaller. The first five teeth of the lower jaw are somewhat conical, especially those most anterior, but all the remaining teeth of both jaws are noticeably laterally compressed and crenulated on their anterior and posterior cutting edges. These crenulations do not show in labial view, because the teeth are slightly convex. The posterior margin of each tooth is somewhat steeper than the anterior margin, and the large central cusp is usually slightly recurved. There are no tricuspid teeth. The upper jaw occludes outside of the lower jaw.

The conical fore teeth in the jaws of both species of chamaeleons hold and prevent escape of the prey. The prey of *Chamaeleo pumilus* falls into all of Hotton's (1955) prey categories of 'low, intermediate, and high activity, and those of light, intermediate, and heavy integument—based on effect of teeth on the integument'. Probably because of its catholic diet, the dentition of *Chamaeleo pumilus* is too complex to fit Hotton's system. In *C. namaquensis* the meticulous chewing shears prey items into neat particles. *C. namaquensis* prey fall into Hotton's (1955) 'heavy integument . . . intermediate activity' prey category. *C. namaquensis* dentition seems most similar to Hotton's Group 'A' dentition, but this is the dentition type of such herbivorous iguanids as *Ctenosaura*, *Dipsosaurus*, and *Sauromalus*. The *Chamaeleo namaquensis* prey would seem to require Hotton's Groups 'D' and 'E' dentitions, but 'D' has little or no lateral compression of the crowns, and neither does 'E' fit, since such teeth are slender and cylindrical. Hotton's other dentition groups do not readily accommodate the teeth of *C. namaquensis*.

Chamaeleon teeth occupy a shallow dental groove in the jaw. Edmund's (1969) description of the number of teeth in *Chamaeleo pumilus* agrees with this study. Chamaeleons have only acrodont dentition, with teeth added only at the most posterior end of the jaw. Chamaeleons lack any anterior pleurodont teeth as in contrast to the agamids, which also have acrodont teeth. Chamaeleonids and agamids do not show the polyphyodonty of other lizards. The teeth of chamaeleonids and agamids apparently wear down with age, until the jaw margin itself is utilized as a cutting edge, but this was never observed.

Sight is the principal sense of chamaeleons, which aim their eyes (see pp. 71–2) on their prey before securing it. Projection of the chamaeleon tongue is a source of dispute between Gnanamuthu (1930) and Zoond (1933). The former thinks projection of the tongue is due mostly to relaxation of the highly contracted hyoglossi. However, by physiological experiments and anatomical investigation of the muscles and vascular supply of the tongue, Zoond (1933) showed that protrusion of the tongue is effected by the contraction of the geniohyoids, the tongue is held protruded by extreme contraction of the hyoglossi, and that several other muscles and tendinous tubes are important in the final thrust and holding of the target. Retraction is by the interplay of the hyoglossi and the sternohyoids. Zoond showed that several points of Gnanamuthu's surmised chamaeleon tongue action are not supported by physiological or anatomical data.

In some *Chamaeleo pumilus* the tongue pulling power approximated two-thirds of the animal's body weight, but most had a tongue pulling power about 50% of their body weight. *C. pumilus* shot its tongue to a maximum range, roughly equivalent to two-thirds of its total length, exceeding the maximal range observed by Von Frisch (1962). In *C. namaquensis* the tongue has a pulling power equivalent to the body weight of the chamaeleon, and was maximally projected to a distance approximating its snout-vent length. Data are limited on the range and pulling power of the tongue of chamaeleons. Dischner (1958) says a Camerounian *C. montium* weighing 100 g has a tongue pulling power of 43 g. As Dischner (1958) observes, there is no evidence of any adhesive substance on the tip of the tongue, other than the 'normal' adhering quality of a moist object. Pulling the tongue from the mouth of an anaesthetized chamaeleon and placing it on a beetle showed no stickiness, neither was it sticky to the touch. The tongue only held an object to which it was forcibly applied, as would be the case in normal projection. The prey is grabbed and held by a mechanical overlapping of the bi-lobed tongue knob (Fig. 8). What is brought in by the tongue was considered food and eaten, even if the missed edible prey was still in view to a chamaeleon chewing a physical surrogate.

2. *Amount of one meal*

Chamaeleo pumilus and *C. namaquensis* in the field were voracious feeders, often eating to stomach capacity, and as soon as the preceding meal passed to the small intestine, a new meal was ingested. Size and specifity in prey selection were important in actual meal volume. Table 18 shows the normal volumetric daily food intake of *C. pumilus* (±70 mm, s-v) and *C. namaquensis* (±105 mm, s-v). By selecting tenebrionids and the smaller orthopterans, *C. namaquensis* realized a greater real intake of food than by taking individually larger prey. While the same was true for *C. pumilus*, the wider tastes of this species made it more difficult for this type of analysis. The largest prey taken by *C. pumilus* adults were tettigoniid orthopterans and large vespids, of which two were capacity. Both of these prey items were Food Index '3' at 2 ml volume each. The smallest prey taken by adult *C. pumilus* were fruit flies (Drosophilidae).

Table 18

Volumetric daily food intake of *Chamaeleo namaquensis*[1] and *C. pumilus*[2].

Example	Prey Food Index	Vol. (ml) each	Number per meal	Daily volume (in ml) per number (in parentheses) of daily meals		
				min.	$\bar{x}$	max.
[1]Large locustid	5,0	4,5	4	(3) 72,0	(6) 108,0	(8) 144,0
[1]Small locustid	4,0	2,0	30	(3) 180,0	(6) 360,0	(8) 480,0
[1]Large tenebrionid	3,8	1,25	19	(5) 118,75	(12) 285,0	(15) 356,25
,, ,,	3,8	1,25	23	(5) 143,75	(12) 345,0	(15) 431,25
[1]Small tenebrionid	3,5	0,85	19	(5) 80,75	(12) 193,8	(15) 242,25
,, ,,	3,5	0,85	23	(5) 97,75	(12) 234,6	(15) 293,25
[2]Muscid	2,0	0,25	15	(3) 11,25	(5) 18,75	(8) 30,0
[2]*Tenebrio molitor*	4,0	2,0	5	(3) 30,0	(5) 50,0	(8) 80,0
,, ,,	4,0	2,0	7	(3) 42,0	(5) 70,0	(8) 112,0
,, ,,	4,0	2,0	10	(3) 60,0	(5) 100,0	(8) 160,0

C. namaquensis and *C. pumilus* began eating soon after emergence—after early morning defecation of the previous late day meal—the former eating prodigiously while drenched in dripping ground fogs, and the latter on frosty winter mornings. Early morning at emergence and late afternoon chamaeleons ate to their stomach capacities. The number of daily meals is given in Table 18. Of 80 *C. namaquensis* stomachs examined, only 2 were empty, and of 150 *C. pumilus* stomachs examined, only 20 were empty.

Wood (1933) and Burrage (1966) studied food amounts ingested by the American iguanid *Uta stansburiana*, noting variation in consumption with the weather, it being greatest at the hottest times of the year. Seasonal variation in food consumption was not particularly noticeable in *C. pumilus* or *C. namaquensis*.

3. *Rates of passage*

Feeding marked insects to chamaeleons showed that the last meal of the preceding day was passed on emergence the following day, which was the longest time for digestion (±12 hours). Digestion of the other daily meals was completed in two to five hours, depending on the integument of the prey. Undoubtedly, the short passage rates reflected the high degree of mastication to which the food was subjected, increasing the area for enzymatic action and absorption.

4. *Prey items*

In *Chamaeleo pumilus* (Table 19) differences in food ingested were seasonal, but appeared to vary with sex. While dipterous families were usually a predominant prey item in both sexes, quite a considerable part of their prey was taken from other insect orders. For example, females ate mostly dipterans (97,2%, mainly muscids) in June, and the least (2%) in October, whereas males ate only dipterans in February, and the least (50%, almost equivalent amounts of syrphids and muscids) in August, with the remaining prey in August almost evenly taken from immature insects (24,5%) and orthopterans (25%). Orthopterous families were predominant in the winter diet of males, whereas the highest intake (23,4%) of orthopterans was in the February diet of females. Essentially as can be seen in Table 19, what was most taken in the diet of one sex for any given month was taken in different amounts by the opposite sex, and the total consumption of each contained different prey elements. Of note was the amount of ground-living carabids taken, which in May accounted for almost a third of the diet of male *C. pumilus*. Greatest ingestion of carabids (22%) by females was in August. *C. pumilus* were found supratidally at Port Nolloth, and The Strand, feeding on small tenebrionids and flies at the former locale, and exclusively on flies at the latter. Injurious insects formed the major portion of the diet of *C. pumilus*, and the large numbers taken rate this little lizard significant in their control.

Table 20 gives the prey taken by coastal *Chamaeleo namaquensis*, and Table 21 that of inland populations. In the former the predominant item was tenebrionid beetles. The lowest amount of tenebrionids in any monthly sample was 60%, and the monthly mean was never below 93,3%. The inland populations of *C. namaquensis* ate larger amounts of other prey items, especially Orthoptera and Lepidoptera. Some prey, such as buprestids and curculionids were seasonally taken, when these were commonest. However, inland *C. namaquensis* also ate predominantly tenebrionids, and the lowest percentage in any monthly sample was 2,5%, and the monthly mean was never below 67%. Plants were ingested regularly, but more so by coastal *C. namaquensis*. In coastal *C. namaquensis* the largest amount of plants in any sample was 29,1%, and the largest mean 2,8%. In inland *C. namaquensis* the largest amount of plants in any sample was 20%, and the largest mean was 1,5%. Certainly some plant ingestion might be incidental with the prey, but this seems scarcely credible in view of the amounts recorded, nor that *Zygophyllum stapffii* was the predominant plant ingested. Only the fleshy parts of these plants were taken in by the chamaeleons. Inorganic matter composed of small stones, gravel, and sand was more frequently ingested by coastal *Chamaeleo namaquensis*, of which the greatest amount in a sample was 30%, and the largest mean was 6,2%. The greatest amount of inorganic matter in an inland sample was 1,1%, and the largest mean was 0,5%. Inorganic matter might be ingested for assisting in internal, physical degradation of food, and/or parasite removal.

The fact that some *C. namaquensis* had eaten larval beetles was interesting,

Table 19

Monthly prey percentage of male and female *Chamaeleo pumilus* at Stellenbosch, Cape Province.

	Jan.		Feb.		March		April		May		June		July		Aug.		Sept.		Oct.		Nov.		Dec.	
Contents	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
Plants	—	0,8	1,3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	17,5	—	2,5	4,0	5,0	1,3	—
Miscellany*	—	—	2,0	—	—	—	—	—	—	—	—	0,4	—	—	—	—	1,0	—	—	5,0	0,6	—	—	—
Unidentified arthropods	—	—	0,5	—	17,2	—	1,0	—	1,4	—	—	1,0	—	—	—	—	2,0	—	—	—	—	0,4	0,2	—
Araneae	—	—	—	—	0,3	0,5	—	—	0,4	—	—	—	2,0	—	—	—	1,5	9,0	—	—	—	2,0	1,8	0,3
Immature insects**	8,0	—	—	—	—	—	—	—	—	—	—	8,0	—	—	—	24,5	—	—	—	—	—	—	0,3	—
Orthoptera	—	—	23,4	—	3,7	7,3	1,7	16,7	6,0	33,3	—	4,0	23,3	25,0	15,0	25,0	14,0	26,0	13,8	—	—	—	—	—
Cicadellidae	1,0	—	—	—	0,3	—	15,0	—	8,6	—	—	—	—	—	2,0	—	2,5	—	—	25,0	6,0	—	7,0	2,5
Psyllidae	5,0	—	—	—	2,5	—	0,3	—	1,0	—	—	—	—	—	—	—	0,8	—	—	—	1,0	2,0	—	—
Aphidoidea	3,0	—	—	—	0,3	—	1,0	—	0,3	—	—	—	—	—	—	—	1,3	—	7,5	—	—	—	0,8	8,8
Lygaeidae	8,0	1,3	—	—	—	—	0,8	5,0	0,9	—	—	—	—	—	—	—	6,3	—	—	5,0	12,0	—	9,2	—
Ichneumonidae	—	—	—	—	—	—	—	—	—	—	—	—	—	12,5	—	—	—	—	—	—	—	—	1,7	1,3
Vespidae	3,0	25,0	21,3	—	—	—	0,2	0,5	—	—	—	—	—	—	—	—	20,5	10,0	24,3	31,0	5,0	—	3,2	3,3
Apidae	—	—	2,4	—	—	—	—	—	—	—	—	4,0	1,6	—	—	—	—	—	—	—	3,4	—	0,5	—
Unidentified Coleoptera	—	—	—	—	—	—	—	—	—	—	0,2	—	—	—	—	—	—	—	—	—	—	—	—	—
Carabidae	8,0	1,3	—	—	—	1,0	—	—	—	30,1	0,2	—	—	—	22,0	0,5	—	—	10,8	—	—	—	0,2	3,3
Coccinellidae	5,0	—	—	—	—	0,7	—	—	—	3,3	0,4	—	—	—	—	—	—	—	5,0	6,5	10,0	—	5,8	3,2
Tenebrionidae	0,3	25,0	—	—	—	0,7	—	—	—	—	—	—	—	—	—	—	7,5	—	2,5	—	—	10,0	5,7	3,0
Chrysomelidae	—	—	—	—	—	1,0	—	—	—	—	1,2	—	—	—	1,0	—	—	—	22,5	—	—	—	4,8	12,2
Curculionidae	29,7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3,3	—	—	—	4,8	4,2
Neuroptera	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2,0	—	0,8	—
Syrphidae	—	1,0	—	—	—	—	3,5	2,0	1,9	—	3,6	—	2,0	27,5	—	25,0	1,3	—	0,5	—	9,6	7,8	7,5	—
Tephritidae	—	0,8	0,3	—	1,2	1,0	0,5	0,5	14,4	—	2,2	—	4,5	—	—	—	—	—	—	—	2,4	6,2	1,3	3,2
Calliphoridae	—	3,8	1,8	1,7	6,3	19,0	2,7	2,5	2,7	—	2,8	2,0	5,2	6,2	3,0	2,0	1,3	—	0,3	—	8,6	5,0	6,7	8,5
Sarcophagidae	—	—	1,5	1,0	4,5	8,4	2,2	1,0	—	—	1,0	—	3,4	1,3	2,0	—	—	—	—	—	6,6	6,6	0,5	—
Muscidae	29,0	41,0	45,5	97,3	63,7	56,7	67,7	71,8	62,4	33,3	87,6	60,6	58,0	27,5	55,0	23,0	40,0	37,5	1,2	25,0	28,8	48,0	35,3	46,2
Lepidoptera	—	—	—	—	—	3,7	3,3	—	—	—	0,8	20,0	—	—	—	—	—	—	8,3	—	—	7,0	0,6	—
Stomachs with food examined	5	4	6	3	6	6	9	8	8	8	10	6	10	5	7	8	7	5	7	3	5	5	6	4
Stomachs empty	2	0	1	0	0	1	2	1	1	4	0	0	1	1	0	1	1	2	1	1	0	0	0	0

— = absent * = shed chamaeleon skin ** = eggs, larvae, and pupae.

Table 20

Prey percentage in given months of a coastal population of *Chamaeleo namaquensis*. The percentage range is shown in parentheses, and when one number is shown it indicates the occurrence of an item in one sample only. The monthly mean is the percentage not enclosed in parentheses.

Contents	February	April	June	November
Inorganic	2,60 (0,01–16,0)	0,56 (0,09–10,0)	6,20 (0,10–30,0)	1,84 (0,20–15,0)
Plants	2,80 (0,01–29,1)	T (0,01–0,2)	0,06 (0,01–1,2)	0,74 (0,01–10,0)
Miscellany*	0,20 (1,0)	T (0,2)	0,02 (0,01–0,8)	T (0,01–0,5)
Unidentified (chiefly arthropods)	T (0,01)	0,01 (0,10–0,3)	0,11 (0,09–4,0)	0,01 (0,50)
Solpugida	— —	T (0,6)	— —	— —
Scorpionida	— —	0,10 (8,0)	— —	— —
Orthoptera	— —	T (0 2)	0,06 (0,05–4,5)	0,82 (0,82–25,0)
Hymenoptera	— —	— —	0,06 (2,0)	0,28 (10,0)
Tenebrionidae	94,60 (70,00–100,0)	99,20 (90,00–100,0)	93,30 (70,00–100,0)	96,34 (60,00–100,0)
Lepidoptera	— —	— —	0,04 (0,05–4,5)	— —
Reptilia	— —	0,14 (1,00–5,0)	0,08 (10,0)	— —
Stomachs examined	10	8	10	11
Scats	20	39	47	32

— = no record.
T = Trace > 0,001.
* = shed chamaeleon skin; various insect orders, mostly Diptera; intertidal arthropods.
N.B. Columns do not quite add up to 100,0% due to trace items and rounding off.

Table 21

Prey percentage in given months of an inland population of *Chamaeleo namaquensis*. The percentage range is shown in parentheses, and when one number is shown it indicates the occurrence of an item in one sample only. The monthly mean is the percentage not enclosed in parentheses.

Contents	February		April		June/August		November	
Inorganic	0,01	(0,50)	—	—	0,18	(0,60–1,1)	0,50	(1,0)
Plants	—	—	—	—	1,33	(0,01–20,0)	1,50	(3,0)
Miscellany*	—	—	0,35	(0,10–3,0)	T	(0,10)	—	—
Unidentified (chiefly arthropods)	—	—	—	—	—	—	—	—
Orthoptera	20,09	(15,00–32,0)	2,00	(3,00–25,0)	—	—	10,00	(20,0)
Buprestidae	—	—	6,25	(25,0)	—	—	—	—
Tenebrionidae	79,09	(60,00–95,0)	66,65	(50,00–99,0)	85,16	(2,50–100,0)	88,00	(76,00–100,07
Scarabaeidae	—	—	6,25	(25,0)	2,73	(38,00–49,0)	—	—
Curculionidae	—	—	—	—	10,25	(24,00–100,0)	—	—
Lepidoptera	—	—	18,70	(99,00–100,0)	—	—	—	—
Stomachs examined**	7		6		22 (2)		6	
Scats	—		10		7		4	

— = no record.
T = Trace > 0,001.
* = shed chamaeleon skin; mammal hair; bird feathers; various insect orders.
** = empty stomachs shown in parentheses.
N.B. Columns do not quite add up to 100,0% due to trace items and rounding off.

since these are mainly fossorial and indicated that *C. namaquensis* occasionally dug up food purposely or ate those unearthed by chance in excavation. It is not known whether the bird feathers and mammal hairs in some inland *C. namaquensis* (Table 21) were the remains of meals or accidental ingestion of feathers and hairs taken in with other prey. Since they were small feathers and hairs, it strongly infers purposeful ingestion of small birds and mammals. A chamaeleon captured at Ganab, near the Great Western Escarpment, had eaten only wasps, but this information is not reflected in Table 21. Some coastal dune-dwelling *C. namaquensis* ate significant numbers of other reptiles (Table 20). In January 1970, at Cape Cross, South West Africa, Dr J. Jurgens collected a chamaeleon that had eaten only reptiles, but this information is not reflected in Table 20. Figure 8 shows a *C. namaquensis* catching a gecko. In the field a male *C. namaquensis* 95 mm long snout-vent was seen to capture and kill a *Bitis peringueyi* 200 mm in total length. At low tide and within the spray of heavy surf, strand-dwelling *C. namaquensis* frequently penetrated seawards of the mean high tide limit on to damp sand. These chamaeleons walked amongst the tidal wrack and fed chiefly on flies, intertidal arthropods, tenebrionids, and reptiles. The ingestion of intertidal arthropods would certainly necessitate a salt gland. Unfortunately, the larger numbers of coastal *C. namaquensis* sampled further inland obscures the actual diet of these strand-dwelling chamaeleons as presented in Table 20.

Burrage (1966) notes that the American iguanid *Uta stansburiana hesperis* takes more flying insects later in the day, when the activity of such forms was restricted to plant cover by increasing wind intensity. *Chamaeleo pumilus* was restricted to plant cover only by the most intense winds, and, at such times, took slightly more flying insects; however, most of its prey was of the winged insect orders. Prey selection by *C. namaquensis* was not affected by wind intensity.

There are no detailed accounts of annual prey ingestion for chamaeleons. Most chamaeleons are insectivorous, though *C. oustaleti* of Madagascar eats mice and birds, and *C. dilepis* and *C. melleri* of Africa take birds (Schmidt & Inger 1965).

5. *Skin-shedding*

Adult *Chamaeleo pumilus* and *C. namaquensis* in the field shed their skins every six weeks, and juveniles every four weeks. Unhealthy chamaeleons took as much as eight weeks between shedding periods, and had difficulty completely sloughing off the old skin. Time interval between sloughing in *C. pumilus* and *C. namaquensis* agrees with Bustard (1963) for *C. chamaeleon*. Shedding was as in *C. dilepis*, as given by Brain (1961). The old skin whitens over the body and limbs prior to shedding. In *C. pumilus* and *C. namaquensis* the old skin splits along the body in a mid-dorsal line and in the neck region and head. By laboured compression, arching of the body, and rubbing against any rough object the skin is loosened and removed. *C. namaquensis* used its hind feet to remove large patches of skin on the back of the body. Both species used their

Fig. 8.

Chamaeleo namaquensis in the act of catching a gecko (*Rhoptropus afer*). Note bi-lobed nature of tip of chamaeleon's tongue, which totally obscures head of victim. Also of interest, this chamaeleon shows Hoesch's 'Schreckmuster' (see text). Photo through courtesy of Mr H. Maedler, Swakopmund.

jaws to remove the old skin from their limbs. Isolated pieces of skin often persisted along the cranial ornamentations for some time. *C. namaquensis* shed its skin almost in one piece, which it then devoured. *C. pumilus* did a more patchy job of sloughing and was less likely to eat the cast skin.

Further aspects of skin-shedding in reptiles are discussed in the following section.

I. *Water and salt balance*

1. *Drinking and water sources*

Chamaeleo pumilus uses its tongue to lap up water drops on plants, but in rains, condensing fog, or drizzle, water drops beading-up on the snout tip were simply run on to the slightly protruded tongue. Occasionally, captives on one twig used the tongue to shoot off water droplets on adjacent leaves. Except during summer, water was readily available to *C. pumilus* in varied forms. In summer, precipitation is less frequent, and at this time dew is the principal source of water. *C. pumilus* always drank early in the day. On rainy days drinking was *ad lib.* through the day, but in clear weather, the early morning drink of dew had to suffice (see water storage and conservation, p. 86).

The water sources available to *C. namaquensis* are the same as that of *C. pumilus*, but the former species rarely encounters rain. Coastal *C. namaquensis* relies mainly on the frequent fogs. On wholly foggy days *C. namaquensis* drinks *ad lib.*, but on clear days fog and dew frequently recurred in the late afternoon and evening when the chamaeleons were still abroad. Thus, on clear days the desert chamaeleon can drink at times early in the day at emergence and late the same day prior to retirement.

C. namaquensis uses its tongue to lap up dew, as well as fog water condensed on vegetation, sand and rocks. It also used the tongue to shoot water drops off adjacent plants. Early in the morning in sparsely vegetated areas, *C. namaquensis* drank from the water-saturated sand arising from condensate run-off from its body. *C. namaquensis* has a fine-grained squamation which serves as fine, very distinct capillary channels leading to the mouth. These channels are especially distinct on the throat and fore-part of the body. If dyed water was placed on the mid-laterum of the body, water moved by capillarity up to the vertebral region, and towards the head and tail. The chamaeleon turned its head to drink the water accumulated on its flanks and vertebral knobs, and in captivity would do so off each other's bodies. Thus, the animal is designed as a 'water collection' surface itself.

Tenebrionid beetles are the principal prey of *C. namaquensis*, and they undoubtedly contribute to the water economy of the chamaeleon. Early in the morning various tenebrionid beetles could be seen upended, with the head buried in the sand and fog water condensing on their thorax and abdomen. The water trickled down to the sand which became thoroughly saturated. Careful removal of the sand around the head showed it to be buried in this water-saturated sand and the jaws working in drinking.

Lizards in areas of moderately high, or regular rainfall, have little difficulty in meeting their water requirements. Most lizards drink essentially as do chamaeleons, but varanids, large iguanids, the larger anguids, teiids and scincids immerse the snout in water to drink. *Chamaeleo pumilus* and *C. namaquensis*, co-inhabitant populations in the Namib Desert at Lüderitz and Port Nolloth, utilize the same water sources. An introduced population of *C. pumilus* at a residence in Walvis Bay had no apparent water-source problem. *C.*

chamaeleon of the Sahara and Levant is the only other chamaeleon of deserticulous habits, but no references to its ecological adaptations have been found. Mayhew (1968) has adequately reviewed water problems of desert lizards. Desert lizards acquire water from: (1) drinking; (2) free water in the food; (3) oxidation water (Schmidt-Nielsen 1964). The helodermatid *Heloderma suspectum* (Bogert & Martin del Campo 1956) needs surface water, and the iguanid *Dipsosaurus dorsalis* and the agamid *Amphibolurus pictus* (Mayhew 1963) copiously drink water if available. *Chamaeleo namaquensis* and *C. pumilus* were both active at times of dew, thus this was a realized water source for them. Since dew occurs on cold nights, most reptiles are considered unable to use this source because they would be inactive (Schmidt-Nielsen & Dawson 1964). However, many desert lizards merely emerge the head, on which the dew may condense and be licked off. The agamid *Moloch horridus* (Davey 1923; Hosking 1923), and iguanids *Phrynosoma modestum*, *P. cornutum*, and *Holbrookia maculata* (Meyer 1966) lick water from plants. Louw & Holm (1972) show the coastal Namib Desert lacertid *Aporosaura anchietae* uses not only condensed fog water directly, but also that condensed on kelp flies.

The hygroscopic skin of the agamids *Cordylus giganteus* (Mertens 1960), *Uromastix hardwickii* (Seshardi 1957) and *Moloch horridus* (Davey 1923) is considered to absorb water by capillary action. Bentley & Blumer (1962) demonstrated that *M. horridus* does not absorb water through the skin, but that the water penetrates fine capillary channels, in which it moves to the mouth and is taken in. Certainly impervious skin would be an advantage to desert forms, and Tercafs (1963) showed variability in dermal permeability of the agamid *Uromastix acanthinurus*, it being permeable when saturated with water, but not in dry air. Warburg (1966) and Maderson (1965*a*) found that the epidermis of some lizards is water permeable. The iguanids *Phrynosoma modestum* (Weese 1917) and *P. m'calli* (Mayhew 1965) have never been observed to drink in the field or in captivity.

2. *Water storage and conservation*

The large urinary bladder was flaccid and empty in all *Chamaeleo pumilus* caught in the late afternoon during dry, summer weather. But *C. pumilus* taken earlier the same day after drinking dew had their urinary bladders distended with fluid (Fig. 9). This observation was also true for those taken on rainy days. These field observations were duplicated in the laboratory and are reported later. It seems that since *C. pumilus* always had access to dew, daily water storage was sufficient to get them through the day during dry, summer weather.

C. namaquensis stores a little water in its digestive tract, though the gut is not visibly distended. The gut was also usually crammed with food, so available space for water storage was limited. The urinary bladder of *C. namaquensis* is surprisingly small (Fig. 10A, B), thick-walled with little expansive qualities, and of negligible use for water storage. Unless *C. namaquensis* uses the vascular space

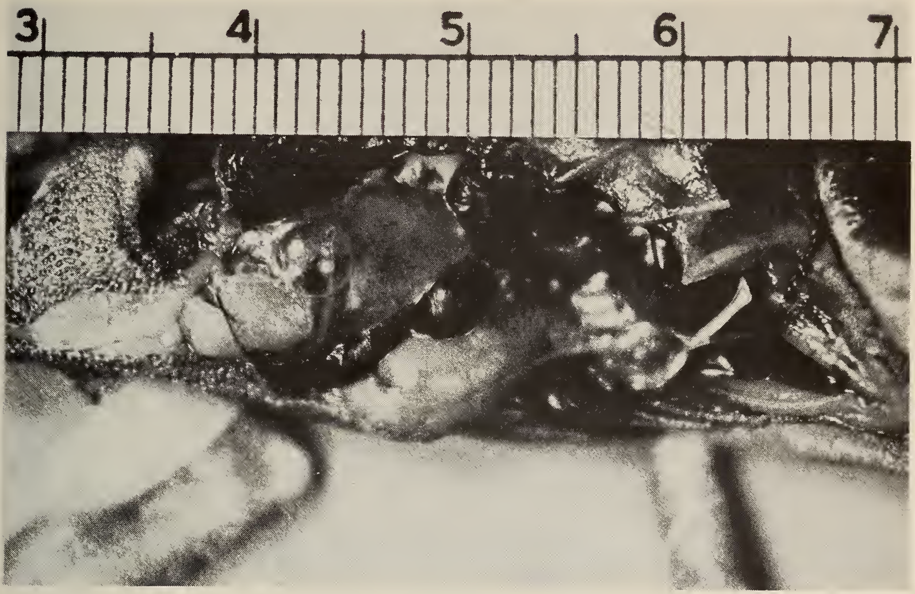


Fig. 9.

Distended urinary bladder of *Chamaeleo pumilus* early on a summer day after drinking dew. Bladder lies approximately between '4' and '5' on mm rule.

for water storage, there seems to be no other visibly apparent water depots. Thus we have the phenomenon of the desert chamaeleon with far less ability to store water than the mesic *C. pumilus*. Coastal *C. namaquensis* apparently obtains sufficient water from the frequent fogs and its food to meet its water requirements. Outside of the fog belt, cloacal reabsorption in conjunction with the salt gland, also allows water economy, and the prey serves as a water source.

Chamaeleo pumilus and *C. namaquensis* excrete a closely packed faeces, which when crushed appeared pasty with hard fragments. The uric acid pellet is excreted first, but attached to the faeces. In these chamaeleons, a water and uric acid mixture can be seen in the ureters. Therefore, it would seem that cloacal reabsorption of water is efficient in both species.

Mayhew (1968) discusses water storage in tissues of desert lizards. Norris & Dawson (1964) found the iguanids *Sauromalus hispidus*, *S. obesus*, and *S. varius* have lateral accessory lymph spaces which are distended with fluid in rainy times and that these storage depots are larger in those forms from more arid regions. The Namib Desert lacertid *Aporosaura anchietae* drinks water copiously and stores it in the digestive tract and vascular space (Louw & Holm 1972). Khalil & Abdel-Messieh (1954) consider the tissues of desert reptiles to have a higher water content than those of mammals, which is disputed by Sokolov (1966).

The gekkonid *Hemidactylus flaviviridis* (Seshardi 1956), agamid *Uromastix*

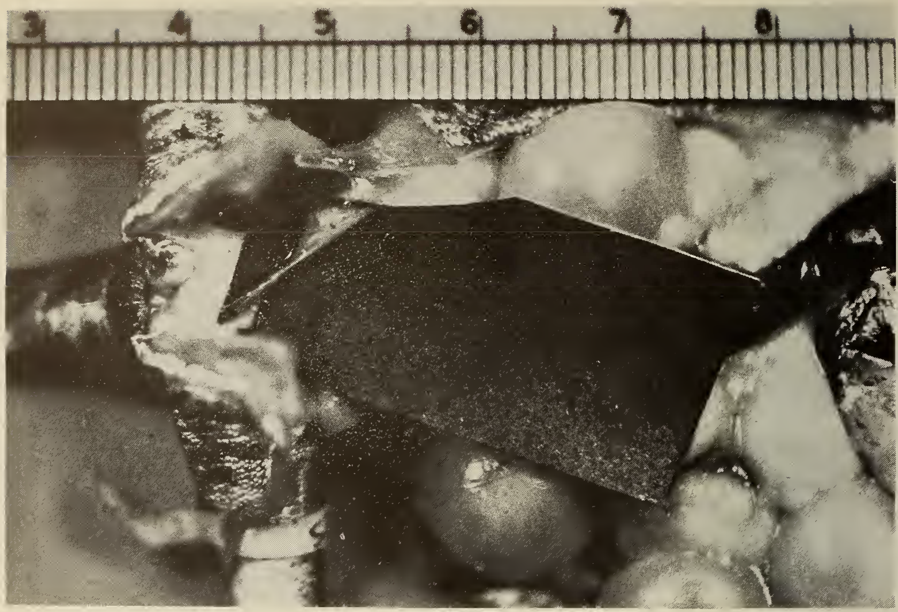
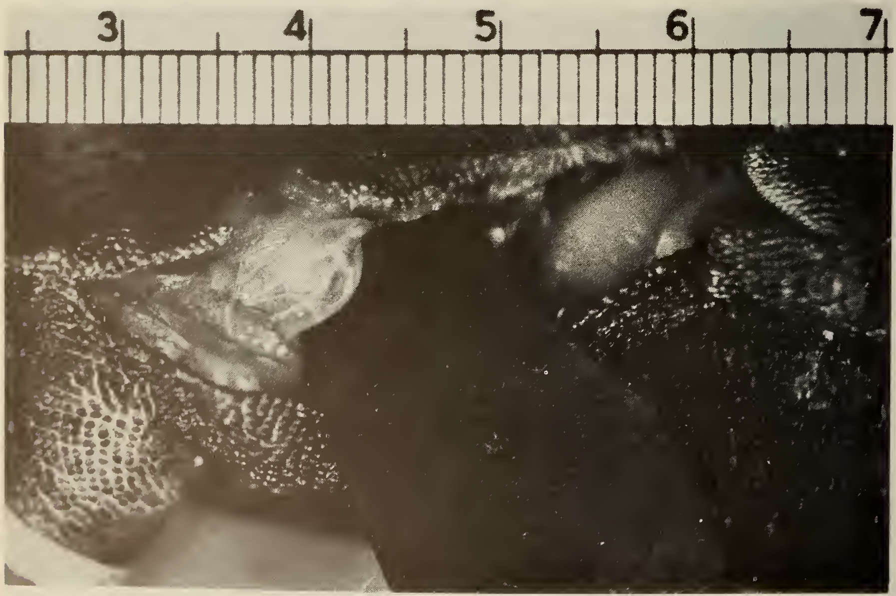


Fig. 10.

A. Flaccid urinary bladder of *Chamaeleo namaquensis*.

B. Distended urinary bladder. In both cases bladder lies directly on top of piece of black paper. Scale in mm.



hardwickii (Seshardi 1957), varanids *Veranus monitor* (Seshardi 1959), *V. gouldii* (Braysher & Green 1970), and scincids *Scincus scincus* and *Chalcides ocellatus* (Khalil 1951) reabsorb water from the urine in the cloaca, excreting the waste as a solid pellet.

3. *Water loss*

Chamaeleo namaquensis was abroad throughout the day, retiring to its retreat only at night. *C. pumilus* is problematical since it occurs in mesic areas, where desiccation is less extreme, but also in arid areas. *C. pumilus* and *C. namaquensis* pant, which is discussed in the section on thermoregulation (see p. 45). Water loss of chamaeleons in laboratory desiccation studies is dealt with in the next section.

Desert reptiles reduce evaporative water loss by avoiding excessively high temperatures, thus diminishing the use of water in temperature regulation (Schmidt-Nielsen 1963). However, Schmidt-Nielsen (1964) noted little evidence that panting involves a great use of water in thermoregulation even at near lethal body temperatures. The rate of water loss in reptiles is slow (Bentley 1959; Warburg 1965*a*, *b*) and is exceeded ten times by that of deserticulous rodents (Chew & Dammann 1961). Some desert lizards utilize the higher humidity and lower temperatures in their burrows during extreme midday conditions (Schmidt-Nielsen & Dawson 1964) as do small desert mammals (Schmidt-Nielsen & Schmidt-Nielsen 1950). Evaporative cooling through the respiratory tract enables reptiles a degree of remaining cooler than their surroundings on hot days (Dawson 1967; Dawson, Shoemaker & Licht 1966) and to dissipate 1,3 times the metabolic heat produced at 44 C in the iguanids *Dipsosaurus dorsalis* (Templeton 1960) and *Crotaphytus collaris* (Dawson & Templeton 1963). At elevated body temperatures oxygen consumption rises and respiration rate increases. As panting ensues, breathing is rapid and monophasic, though oxygen consumption decreases at higher temperatures (Dawson & Templeton 1963; Templeton & Dawson 1963; Dill, Edwards, Bock & Talbott 1935). Consulting Table 16 indicates these relationships to be true for *Chamaeleo namaquensis* and *C. pumilus*, particularly the former.

Benedict (1932), Templeton (1960), and Dawson & Templeton (1963) found evaporative water loss is in excess of water produced, so lizards are dependent on preformed water from their food for maintaining water balance. Since lizards are uricotelic, they gain more oxidation water from protein degradation than ureotelic forms (Schmidt-Nielsen 1964; Schmidt-Nielsen & Dawson 1964). Thus, carnivorous saurians gain considerable water from their prey. Reptiles cannot form hypertonic urine. Roberts & Schmidt-Nielsen (1966) found the kidneys of the iguanids *Phrynosoma cornutum* and *Tropidurus* produce isoosmotic urine, reabsorbing 55% of the glomerular filtrate. Chew (1961) and Bradshaw & Shoemaker (1967) found dehydrated lizards may excrete little urine, but their blood tolerates a greater sodium increase, resulting from electrolyte retention. Shoemaker, Licht & Dawson (1966, 1967) and Dawson

(1967) found the scincid *Tiliqua rugosa*, the gekkonid *Phyllurus milii*, and the agamid *Amphibolurus barbatus* excrete water loads with the least loss of sodium near their particular thermal preferenda. Maderson (1965*b*) hypothesized that skin-sloughing may enable lizards to excrete wastes without losing water.

Chew (1961) and Chew & Damman (1961) considered the skin of some reptiles to be nearly waterproof. However, cutaneous water loss recently has been shown to be a significant avenue of loss, often exceeding that lost via respiration and excretion. Of several reptiles from habitats of varying degrees of aridity, *Sauromalus* (most arid) lost the least (5% of *Caiman*). Cutaneous evaporation in *Sauromalus*, however, was the chief avenue of loss, accounting for 66% of the total water loss at 23 C. Other examples of cutaneous evaporative loss as a percentage of the total water loss are: the arid-dwelling iguanid *Uta stansburiana* 39% and the more humid iguanid *Anolis* 42%—at 30 C (Claussen 1967), at 30 C, 57% in the gekkonid *Gehyra variegata*, and 59% in the agamid *Amphibolurus ornatus*, and at 20 C, 70% in both of the preceding forms (Dawson *et al.* 1966). Maderson (1964) feels the main site of cutaneous water loss in reptiles is the hinge area around the scales. Temperature controlled water loss is that via respiration, and the humidity affects the rate of cutaneous water loss (Warburg 1966).

4. *Laboratory desiccation studies on Chamaeleo pumilus and C. namaquensis*

Table 22 shows the body weight losses of the chamaeleons without food or water for seven days and Table 23 gives the haematocrits and plasma osmolality values (with the significance at 'P' level) of the de- and rehydrated groups of this experimental set of *Chamaeleo pumilus* and *C. namaquensis*. Significant differences in the haematocrit are shown between dehydrated *C. pumilus* and dehydrated *C. namaquensis*; between dehydrated *C. pumilus* and *C. namaquensis* and those rehydrated. There is no significant difference between

Table 22

Weight changes (in grams) of ten *Chamaeleo pumilus* and ten *C. namaquensis* desiccated for seven days, giving body weights at the start and the conclusion of dehydration, body weight losses during dehydration, and body weight changes after rehydration. Means are shown in parentheses.

		Dehydrated body weights		Rehydrated body weights
	In	Out	%loss	at death
Dehydrated				
C. pumilus	8,0–12,4 (10,3)	6,2–10,8 (8,5)	16,8–29,0 (21,7)	
C. namaquensis	17,8–82,3 (55,5)	15,8–77,0 (52,0)	4,6–12,4 (7,1)	
Rehydrated				
C. pumilus	6,4– 9,5 (8,4)	5,3– 7,9 (7,0)	13,1–22,6 (16,7)	6,2–10,2 (8,7)
C. namaquensis	49,7–90,1 (60,7)	45,9–84,9 (56,2)	2,3–12,3 (7,6)	47,2–88,0 (57,8)

rehydrated *C. pumilus* and *C. namaquensis*. In plasma osmolality values there is a significant difference between dehydrated *C. pumilus* and dehydrated *C. namaquensis*, and between dehydrated and rehydrated *C. pumilus*, but no significant difference between rehydrated *C. pumilus* and *C. namaquensis*, nor between dehydrated and rehydrated *C. namaquensis*. These data suggest a degree of water storage in the vascular space of both chamaeleons.

Table 23

Haematocrits, and plasma osmolalities, with relevant statistics for ten *Chamaeleo pumilus* (Cp) and ten *C. namaquensis* (Cn) subjected to seven days' desiccation at 0% humidity. At day seven, the rehydrated half of each group were killed and the remainder then rehydrated and killed the following day.

	Haematocrits	Dehydrated	Rehydrated
Dehydrated			
Cp . . .	28,6–33,7 ($\bar{x}$ = 31,3; S.D., 2,4)	Cn^{a} P = <0,001	
Cn . . .	14,6–19,8 ($\bar{x}$ = 17,6; S.D., 2,3)		
Rehydrated			
Cp . . .	14,5–29,0 ($\bar{x}$ = 21,4; S.D., 6,0)	Cp$^{a, b}$ P = >0,2	Cn$^{a, b}$ P = >0,2
Cn . . .	15,5–32,5 ($\bar{x}$ = 24,6; S.D., 7,4)	Cn$^{a, b}$ P = >0,2	
Dehydrated			
Cp . . .	395–440 ($\bar{x}$ = 421,3; S.D., 19,0)	Cn$^{a, b}$ P = >0,2	
Cn . . .	230–255 ($\bar{x}$ = 246,3; S.D., 11,1)		
Rehydrated			
Cp . . .	200–210 ($\bar{x}$ = 203,8; S.D., 4,8)	Cp^{a} P = <0,05	Cn$^{a, b}$ P = >0,2
Cn . . .	219–292 ($\bar{x}$ = 261,3; S.D., 35,4)	Cn$^{a, b}$ P = >0,2	

The results of the experiment on the survival of *C. pumilus* and *C. namaquensis* with food but no water for twelve days and food and water for an additional three days are given in Tables 24 and 25. Due to the difficulty in acquiring sufficient numbers of *C. namaquensis* in respect of all the studies conducted, the numbers here are too small for statistical analysis. The striking feature is the mortality of half of the *C. pumilus* by the sixth day and the badly dehydrated state of the survivors at the end of the dehydration period. The two taken for an additional three days with water quickly recovered some of their weight loss. Even the deserticulous *C. namaquensis* showed some dehydration and had one mortality, from unknown causes, during the experiment. All of the rehydrated *C. namaquensis* showed an increase in body weight on the first day of rehydration, but at sacrifice had lost more than they had gained, despite having food and water. Both species ate less without water, and easy faecal elimination seemed hindered. The haematocrit and plasma osmolality values of the dehydrated and rehydrated chamaeleons in this experiment approximated those given for the chamaeleons in the preceding experiment.

Upon rehydration in both experiments *C. pumilus* strained and ran to the water, drinking so fast that it choked, and regurgitated, but kept drinking until satiated. *C. namaquensis* acted likewise, but it also chewed water-saturated vegetation, which it spat out, and rolled, ploughed, and rubbed its body in wet sand. Upon sacrifice, both sets of rehydrated chamaeleons contained considerable ingested water, especially evident in the urinary bladder of *C. pumilus*, and the digestive tract and urinary bladder of *C. namaquensis*.

Freshly caught *C. pumilus* (elev. 105 m) had a haematocrit of 29,0–30,5 (N = 7; x̄ = 29,9; S.D.; 0,63), and plasma osmolality values of 200–210 (N = 8; x̄ = 203,8; S.D.; 5,23). Freshly caught *C. namaquensis* had haematocrits of (coastal; elev. 12 m) 42,0–49,0 (N = 10; x̄ = 44,5; S.D.; 2,28), (inland; elev. 407 m) 46,0–50,0 (N = 7; x̄ = 48,7; S.D.; 1,38), and plasma osmolality values of 220–290 (N = 8; x̄ = 259,8; S.D.; 28,64). The wide range of the S.D. of the plasma osmolality values of *C. namaquensis* may reflect individual differences, the fact that the sample did not separate inland and coastal specimens, or the delay in sacrificing the animals.

Table 24

Body weight losses (in grams) for 3 day periods for 8 *Chamaeleo pumilus* (Cp) and 8 *C. namaquensis* (Cn) for 12 days with food but no water. At the end of 12 days, 2 *C. pumilus* and 6 *C. namaquensis* were given water and food for an additional 3 days (see Table 25). Means are shown in parentheses.

	Days						
	1–3	4–6	7–9	10–12	Body weights		
	Body weight losses				In	Out	% loss
Cp	0,8–1,5 (1,1)	0,6–1,3 (0,9)	0,4–0,8 (0,5)	0,3–0,5 (0,4)	6,1–11,3 (8,7)	3,4– 8,6 (6,2)	23,9–44,3 (29,9)
Cn	0,5–4,9 (2,1)	0,4–4,3 (1,5)	0,3–3,2 (1,6)	0,4–1,6 (0,9)	36,0–91,4 (60,8)	31,0–77,4 (54,9)	3,3–15,3 (9,6)

Table 25

Weight changes (in grams) of *Chamaeleo pumilus* (1–2) and *C. namaquensis* (3–7) which were given water and food for 3 additional days after receiving only food for 12 preceding days (see Table 24).
Days 13 to 15

Id. No.	Body weight In	Body weight Out	Rehydration Maximum body weight (day in parentheses)	3 days Total losses Uric acid	3 days Total losses Faeces	Remarks
1	12,5	14,0	14,0 (15)	0,12	0,67	
2	8,5	9,2	9,2 (15)	0,06	0,22	
3	50,5	50,3	53,3 (13)	0,16	1,32	
4	48,5	48,8	49,2 (13)	0,28	2,91	
5	49,0	47,5	50,0 (13)	0,31	0,80	shed skin day 13
6	60,3	60,1	62,0 (13)	0,17	1,98	
7	77,4	73,7	79,3 (13)	0,67	3,40	shed skin day 13

Water is obviously crucial to chamaeleons, as was first observed by Brehm (1893), latterly by Bustard (1963), Von Frisch (1962), and experimentally shown in this study. Starving and dehydrated chamaeleons, as those shipped a distance, will drink before they feed, even if food is abundant. They cannot survive on food alone, as the laboratory tests demonstrate. Even humidities of 40–50% experienced by the animals given food and no water did not assuage them, yet this humidity was experienced by them in the field, and actually a trifle low for coastal *C. namaquensis*.

Minnich (1970) estimates that *Dipsosaurus dorsalis* loses via defecation 61% of its total water intake, and water loss studies under simulated natural conditions apparently show that this iguanid cannot balance evaporative water loss through oxidative water production at the low humidities it encounters when active. A loss via defecation of 61% of the total water intake seems a bit high in the light of studies on cutaneous water loss in reptiles. Perhaps *D. dorsalis* has less cutaneous water loss than another desertic iguanid, *Sauromalus*, though it seems doubtful. Comparison of chamaeleons with other reptile desiccatory studies is difficult, since the dehydration period varies. Claussen (1967), for example, kept his animals in the drying chamber for only 24 hours. Furthermore, he was able to collect faecal and uric acid eliminations in a manner not possible in this study. Faeces and uric acid were weighed as promptly as possible, while they were still moist and freshly eliminated. However, such data seem too open to variables and, thus, are not given here.

Louw & Holm (1972) found *Aporosaura anchietae* haematocrits (dehydrated) of 43–48 ($\bar{x} = 45$); (rehydrated) 41–46 ($\bar{x} = 44$), and osmolality values (dehydrated) of 410–435 ($\bar{x} = 420$); (rehydrated) 390–415 ($\bar{x} = 406$), and 'normal' of 275–320 ($\bar{x} = 312$). Freshly caught and rehydrated *Chamaeleo pumilus* haematocrit values agree with those (26,0–35,0; $\bar{x} = 29{,}7$) given by Thorson (1968) for terrestrial sauria, but those for rehydrated *Aporosaura anchietae* (Louw & Holm 1972) and for this study for normal and rehydrated *C. namaquensis* do not. This may be due to Thorson's use of the tropical, non-arid saurian, the green iguana (*Iguana*); however his values (25,0–34,0; $\bar{x} = 29{,}6$) for the deserticulous tortoise (*Gopherus*) are still much lower than those for the desert-dwelling *Aporosaura anchietae* and *Chamaeleo namaquensis*. Thorson notes the similarity in haematocrit values of those reptiles inhabiting the two desiccatory environments of sea and land, and deserts are the most drying.

5. *Salt balance*

Figure 11A, B shows a close-up of the salt exudate around the nares of a captive juvenile *Chamaeleo namaquensis*. In *C. namaquensis* the salt gradually exudes in the manner of a brine, forming a considerable deposit as it dries, through which runs a small air passage. When the encrustation gets too large, it is rubbed off with the feet or by scraping the nose against some object. Though *C. pumilus* inhabits supratidal bushes and may ingest animals with a high salt content, no evidence of salt excretion was observed for this species. Collected from *C. namaquensis*, the dry salt exudate was dissolved in 0,1 ml of distilled water. The exudate contained 7 mEq/L of potassium; 45 mEq/L of sodium; and 49 mEq/L of chloride. While captive *C. namaquensis* occasionally ingested water-drenched plants, especially succulents, for water, those in the field not infrequently had plant matter (see food habits, p. 79) in their digestive tracts. The finding of potassium in the nasal salt exudate may indicate

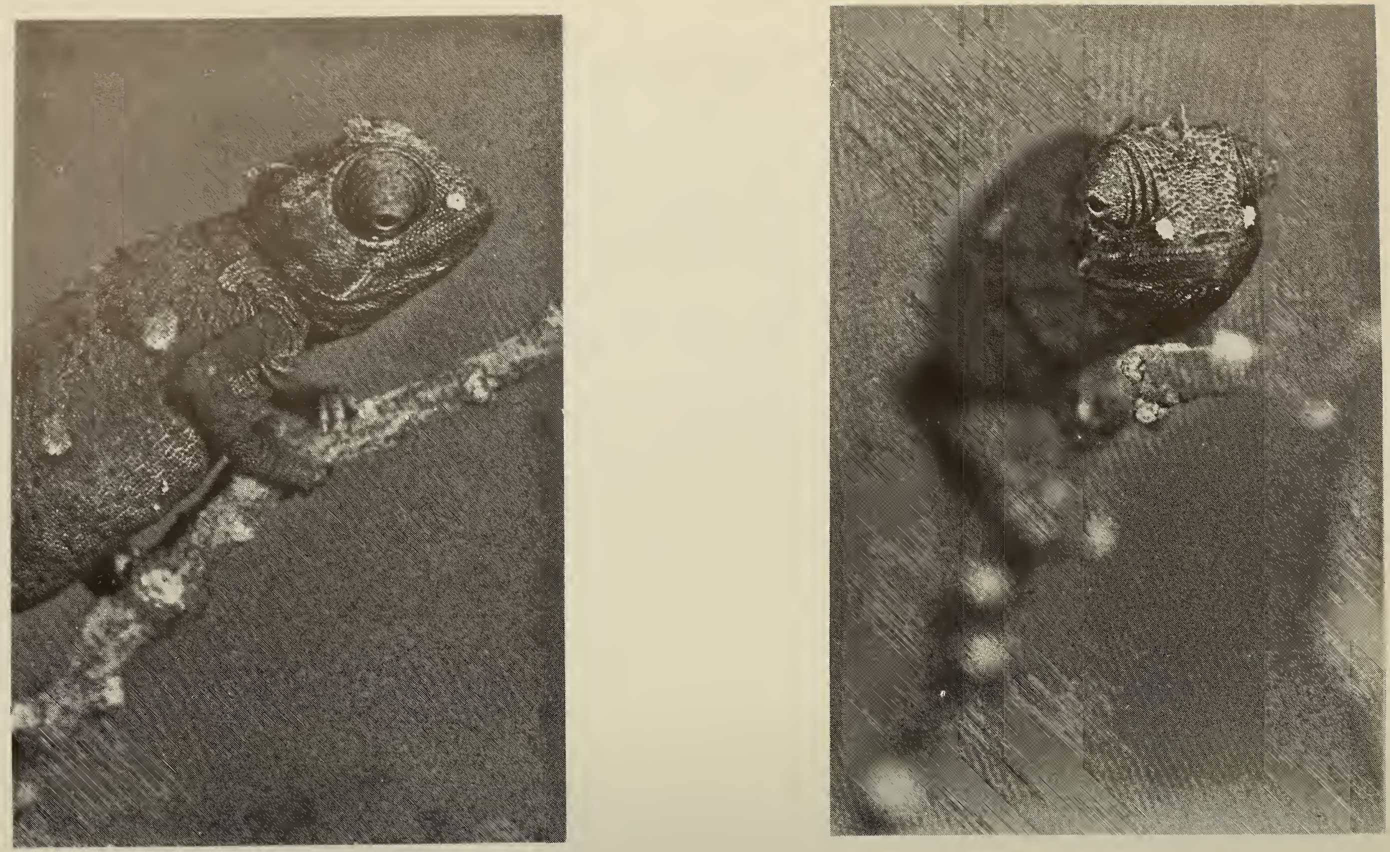


Fig. 11A–B.

Close-up views of nasal salt exudate in *Chamaeleo namaquensis*. Note air passage in Fig. 11A.

an ability to utilize desert plants for food às well as water. Either way it is most interesting, since we may have an omnivorous chamaeleon, excreting salts extrarenally as an adaptation to diet and utilization (plant-chewing) for maintaining water balance. Several lizards (Neill 1958; Burrage 1966) prey intertidally on marine arthropods along desert shores, and undoubtedly take in with such prey some quantity of salt which must be eliminated. *C. namaquensis*, inhabiting the Namib Desert littoral, is the only chamaeleon known to exploit this niche.

Schmidt-Nielsen (1963) feels extrarenal salt excretion is related to cloacal water reabsorption. This may be necessary for production of a low water content urine and efficient cloacal water conservation. The cations of sodium and potassium are actively reabsorbed, with water following passively, which method requires far less work than active water transport. The salt gland serves, then, to eliminate excess cations, which would be primarily potassium in herbivorous and sodium in carnivorous forms.

Schmidt-Nielsen (1965) gives a good general physiological and anatomical account of salt glands; Roberts & Schmidt-Nielsen (1966) also describe the structure of the gland. The reptile salt gland is structured as that of other vertebrates, with branching secretory tubules arranged radially around a central duct. Most studies on salt-excreting saurians have been done on herbivorous forms, which excrete primarily potassium. Templeton (1963, 1964) showed the iguanids *Ctenosaura pectinata* and *Sauromalus obesus* excrete 950 mEq/L of potassium at 190 times plasma concentration, being similar to renal tubule secretion in mammals. Potassium predominates even when the animals were injected with sodium chloride. Other salt-excreting saurians are *S. hispidus*, *S. varius* (Norris & Dawson 1964), *Dipsosaurus dorsalis* (Schmidt-Nielsen, Borut, Lee & Crawford 1963; Templeton 1966), agamids *Uromastix aegyptus* (Schmidt-Nielsen *et al.* 1963), *U. acanthinurus* (Grenot 1967), and the non-arid-dwelling tropical iguanid *Iguana iguana* (Schmidt-Nielsen *et al.* 1963) which secretes potassium as a bicarbonate. These lizards are all primarily herbivorous and the salt-excreting gland serves to remove the salt loads, of which potassium is the major cation, derived from the halophytes on which they feed, which cannot be excreted by their kidneys. Norris & Dawson (1964) consider excretion of potassium by the salt gland of *Sauromalus varius* a physiological adaptation of deserticulous herbivorous lizards to utilization of halophytic plants.

J. *Population structure*

1. *Density and biomass*

The high survival of adult *Chamaeleo pumilus* (Table 26) and *C. namaquensis* (Table 27) suggests the very young either bore the brunt of predation or were harder to locate. Adult *C. pumilus* were recovered at a higher rate than juveniles, though after two to three months the juvenile recovery rate stabilized, thus indicating a high mortality of the very young. Of 40 juvenile and adult *C. pumilus* marked in February 1969, 40,0% were recovered in February 1971.

Table 26

Number of *Chamaeleo pumilus* adults and juveniles marked each month (vertical column) and subsequently recovered in later months (horizontal column). As juveniles of a given month mature they are included with the adults of that month.

Percentage recovered in

	N marked		Mar.		Apr.		May		June		July		Aug.		Sep.		Oct.		Nov.		Dec.		Jan.	
	Ad't	Juv.	Ad't	Juv.	Ad't	Juv.	Ad't	Juv.	Ad't	Juv.	Ad't	Juv.	Ad't	Juv.	Ad't	Juv.	Ad't	Juv.	Ad't	Juv.	Ad't	Juv.	Ad't	Juv.
Feb.	20	20	50	60	65	35	35	30	45	40	40	30	65	40	65	0	90	0	55	0	0	0	55	0
Mar.	25	30	—	—	52	33	24	0	32	13	36	13	56	33	36	20	68	33	56	0	60	0	33	0
Apr.	17	10	—	—	—	—	59	60	29	20	29	50	35	50	29	50	41	40	53	30	47	0	29	0
May	15	8	—	—	—	—	—	—	60	50	60	37	53	37	53	50	47	25	60	32	33	25	47	0
June	20	1	—	—	—	—	—	—	—	—	40	0	50	0	15	0	55	0	35	0	40	0	40	0
July	9	0	—	—	—	—	—	—	—	—	—	—	67	0	67	0	44	0	44	0	22	0	44	0
Aug.	13	0	—	—	—	—	—	—	—	—	—	—	—	—	54	0	38	0	38	0	8	0	0	0
Sep.	15	20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	53	25	27	20	0	40	33	85
Oct.	53	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	45	0	28	0	26	25
Nov.	2	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	100	0	0
Dec.	141	25	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	31	60
Jan.	10	23	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Of 11 coastal juvenile *C. namaquensis* marked in June, overall recovery in November was only 27,2%, of which all were males, for a male recovery of 45,4%. Of the 41 coastal juveniles marked in November, 48,7% were recaptured in February. Of 21 males marked in November, 52,3% were recovered in February. In February, 45,0% of the females were recovered, of the 20 marked in November. Only in February did marked juveniles (53,4%) exceed adults, though since these juveniles were all coastal, they were actually a larger component of this population (58,5%).

Of 207 marked *C. namaquensis* adults, only 17 were not definitely maintaining territories. As the number removed for research purposes is not included, the biomass (mean weight of chamaeleons per hectare) of *C. namaquensis* (Table 27) and *C. pumilus* (Table 28) could be considered somewhat above what is given.

Table 27

Mean density per hectare, body weight, and biomass (in grams) of juvenile and adult *Chamaeleo namaquensis* based upon a composite of two study stations.

	Monthly total marked (recovered and new)				Per hectare		Percentage of adult recovery marked in		
	Adults	Mean weight	Juveniles	Mean weight	Density	Biomass	April	June	Nov.*
Apr.	45,0	37,5	—	—	0,5	18,8	—	—	—
June	56,0	53,8	11,0	7,0	6,1	70,8	43,2	—	—
Nov.	57,0	56,1	41,0	3,5	21,2	111,0	24,3	40,0	—
Feb.	49,0	65,3	55,0	8,0	23,4	238,8	40,5	36,0	20,8
Mean	51,8	53,1	35,6	6,1	12,8	109,9			

* Months at far left should be read for recovery month of adults. Juvenile recovery is discussed in the text.

Table 28

Mean density per hectare, body weight, and biomass (in grams) of adult and juvenile *Chamaeleo pumilus* based upon a composite of all study stations. (See Table 26 for percentage recovery per month.) N.B. As juveniles of a given month mature they are included with the adults of that month.

	Adults	Mean weight	Juveniles	Mean weight	Total Density	Biomass
Feb.	20	13,5	20	1,0	40	290,0
Mar.	35	8,5	42	1,5	77	361,0
April.	43	7,4	34	1,7	107	363,7
May	38	8,8	20	1,5	58	364,4
June	51	11,0	16	1,6	67	586,6
July	48	11,5	18	1,7	66	582,6
Aug.	70	6,5	29	1,8	99	507,2
Sept.	66	10,5	35	0,6	101	714,0
Oct.	120	9,3	35	1,0	155	1 151,0
Nov.	89	9,3	22	0,6	111	846,3
Dec.	195	12,5	39	0,5	234	2 456,0
Jan.	118	9,5	56	0,8	174	1 165,8
Mean	75,2	9,9	29,6	1,3	107,4	802,0

Biomass of *Chamaeleo pumilus* was highest in December, no doubt reflecting the increasing proportion of young and older juveniles. It is not certain whether the slow climb from February to May is best assigned to an increase in marked individuals, a reflection of actual conditions, or both factors. Biomass of *C. namaquensis* was highest in February. But that of adults was relatively consistent; monthly variations merely reflecting increased weights of reproductively active adults, and addition of juveniles. Since juveniles were not territorial and were tolerated in the territories of the adults, biomass of juveniles in a given area often exceeded that of adults.

The density of *C. pumilus* varied with habitat, being densest on reeds surrounding still bodies of water, as vleis, and least in brushy areas. Density in brushy areas never exceeded 12 ($\bar{x} = 8$) per hectare, of which males composed approximately 45% of the population. In reedy areas densities ranged from 75 to 200 ($\bar{x} = 90$) per hectare, of which males were 40–51% ($\bar{x} = 47\%$) of the population. These data are not reflected in the tables. Differences in habitat density for *C. namaquensis* are apparent in Tables 32 and 33, but these data are somewhat misleading, since more time was spent at coastal locales. Also, there is a big difference between 'inland' and 'coastal' dunes. Inland dunes have vegetation-covered hummocks at their bases, which are lacking in coastal dunes which only have very meagre and scattered single grasses, predominantly *Eragrostis spinosa*. Because these inland vegetated hummocks were on true dunes, they were considered to be part of the dunes, whereas coastal vegetation-covered dune hummocks were accumulations of dune sand on flat areas, apart from dunes. Though found throughout the desert, *C. namaquensis* was most numerous in topographically varied areas.

In February juvenile *Chamaeleo pumilus* (Table 29) were at parity with the adults and in March 56% of the population, and least evident (16,8%) in

Table 29

Population structure (in per cent) of 346 adults and 148 young in the marked population of *Chamaeleo pumilus*. Large follicles are those having a diameter of 5 mm or greater.

	Females					
			Yolked follicles		Males	
Month	Juveniles	Pregnant	Large	Small	Active	Inactive
Feb.	50,0	12,5	0,0	20,0	17,5	0,0
Mar.	54,5	15,6	5,2	9,1	15,6	0,0
Apr.	38,5	5,7	27,2	5,7	12,9	10,0
May	34,5	13,8	8,6	8,6	20,7	13,8
June	23,9	17,9	11,9	11,9	4,5	29,9
July	27,3	33,3	10,6	0,0	0,0	28,8
Aug.	30,0	34,0	5,0	4,0	27,0	0,0
Sept.	34,0	23,0	8,0	10,0	22,0	3,0
Oct.	22,6	28,4	6,5	8,3	30,3	3,9
Nov.	19,9	25,2	13,5	6,3	35,1	0,0
Dec.	16,8	16,8	12,8	13,7	39,0	0,9
Jan.	32,3	23,7	3,5	4,2	36,3	0,0

December. *C. pumilus* males were usually slightly in the minority (see also Hogben & Mirvish 1928*a*, *b*; Zoond & Eyre 1934), and in some months males were outnumbered by a considerable margin. Only in November were female *C. pumilus* greatly outnumbered by males. Juvenile *C. namaquensis* (Table 30) were predominant in February (58,5% coastal; 53,4% overall) and a significant component in November. Tables 27 and 30 reflect overall, rather than one population data. Male *C. namaquensis* were somewhat more predominant in June and November, almost at parity with the females in August (inland data only), and the minority sex in February and April.

Table 30

Population structure (in per cent) of 207 adults and 107 juveniles in the marked population of *Chamaeleo namaquensis*. Large follicles are those having a diameter of 5 mm or greater.

		Females			Males	
			Yolked follicles			
Month	Juveniles	Gravid	Large	Small	Active	Inactive
Feb.	53,4	2,8	18,2	3,7	21,1	0,8
Apr.	0,0	40,0	0,0	17,8	42,2	0,0
June	14,2	12,9	6,5	24,6	41,5	0,0
Nov.	41,8	9,2	14,3	9,2	19,4	6,1

Over 27 months Bourgat (1968*a*) marked 140 *Chamaeleo pardalis* on Réunion Island, of which 80 were lost, 54 recovered over several subsequent weeks, and six recovered several months later. Unlike *C. pumilus* and *C. namaquensis*, *C. pardalis* males outnumbered females 6:1, males being most abundant in December to April, but tend to hibernate in cooler times, whereas females are in evidence throughout the year. Bourgat observed 632 males, 382 females, and 31 young. No young were uncovered in January, April to June, and August. There are no other ecological field studies on chamaeleons, and in this respect, statements of chamaeleon population structure are rather premature.

The spatial relationships of American saurians, especially iguanids, have been the most studied, and good reviews are those of Rand (1967), and Mayhew (1968). However, almost all of these are of no comparative value for *Chamaeleo pumilus*, since the iguanids studied are not arboreal, and of doubtful value for *C. namaquensis*. Most studied saurians have an almost 50:50 sex ratio. Population density has been thoroughly investigated in *Uta stansburiana* and related insular forms of *Uta* (Soulè 1964); *U. s. hesperis*, *U. stejnegeri*, and *U. elegans* (Burrage 1966); *U. s. stansburiana*, and *U. stejnegeri* (Tinkle 1961, 1967; Tinkle, McGregor & Dana 1962; Tinkle & Woodard 1967). The average inland density is approximately 25,5 territory-holding adult utas per acre (about 63,6 per hectare), while that of littoral and insular populations is two to three times as dense. Very few tropical species have been studied, but Harris (1964) reports of 36 *Agama agama* per acre (about 90,0 per hectare) with a biomass of about 2 000 grams (about 5 000 g per hectare). According to Cagle (1946), *Hemidactylus* on Tinian have a density of 500 adults in a 2 400 square feet area (about 223,0 m^2), so assuming even distribution this gives 10 000 per acre (about 25 000 per hectare). Larger species have lower densities and all sizes of tropical species the highest. Shore-dwelling and insular populations have higher densities than those inland, even those adjacent to the coast.

Data are meagre on survival of lizard populations and those available indicate widely different demographies in different species populations. Almost all are concerned with temperate iguanids, save the tropical *Basiliscus* and *Anolis*; *Cnemidophorus* (temperate) and *Ameiva* (tropical) are teiids, and *Amphibolurus* is an Australian agamid. Blair (1960), calculating on theoretical natality rather than juveniles actually marked, estimated that 6–20% of hatchling *Sceloporus olivaceus* reached maturity and 20% of the adults survived to a second breeding season. Fitch (1956) reports almost 40% of young *Crotaphytus collaris* reach sexual maturity, about 20% of these surviving a second season. Crenshaw (1955) reports *Sceloporus undulatus* hatchlings suffered a 50% loss during their first six weeks, and 68% in their first two months; a mortality schedule similar to that reported for *Uta stansburiana* by Tinkle (1967). Burrage (1966) observes that the brunt of predation is borne by the very young and adult females in *U. s. hesperis*. Less than 10% of *Basiliscus vittatus* and *Ameiva quadrilineata* live for one year and only 2% of *Basiliscus* survive two years (Hirth 1963). Essentially, annual turnover is suggested in *Anolis limifrons* (Sexton, Heatwole & Meseth 1963) and *Amphibolurus isolepis* (Storr 1965), but these are based on size groupings present at different times of the year, rather than recovery of marked animals. Fitch (1958) records a 50% yearly reduction of adult *Cnemidophorus sexlineatus*.

2. *Social interactions*

Chamaeleo pumilus defended only its perches and such territorial conflicts were noted in all months at homo- and heterosexual levels. There were more such disputes between females in winter, more between males in summer, though overall territorial disputes were seasonally constant. Table 31 documents

Table 31

Number of social interactions observed in the field in coastal and inland populations of adult *Chamaeleo namaquensis*. (Table is set up to show the defender on the left *versus* the transgressor on the right, hence the two sets of heterosexual combat.)

		Social Interactions				
		Territorial conflicts				Copulation
Month		♀♀ *vs.* ♀♀	♀♀ *vs.* ♂♂	♂♂ *vs.* ♂♂	♂♂ *vs.* ♀♀	♂♂ and ♀♀
Feb.	Coast	17	0	12	0	0
	Inland	6	0	2	0	1
Apr.	Coast	51	14	43	10	104
	Inland	0	0	0	0	0
June	Coast	15	1	10	0	5
	Inland	5	1	0	2	7
Nov.	Coast	0	0	3	3	0
	Inland	0	0	0	0	0

C. namaquensis social interactions in the field at various contact levels. The territorial structure of *C. namaquensis* was such that interactions were between neighbouring individuals mainly on the finely delimited borders of their respective territories. They often inflicted considerable damage on each other in such defence. As defenders, females were involved in more homo- and heterosexual territorial defence than males, but were not observed in any in November, and no heterosexual combat in February. Males defended their territories throughout the year, but were not observed to engage in heterosexual disputes in February. Courtship and coition in both species is discussed under courting in the reproduction section (see p. 111).

3. *Territorial display*

Territorial displaying *Chamaeleo pumilus* gorged the throat, which had orange interstitial skin in Stellenbosch specimens, but purple in those from Port Nolloth. *C. pumilus* laterally compressed the body which assumed Colour Index '5' and facing-off delivered a series of five side-to-side head bobs in a right and left horizontal 'T', starting and finishing on the right. Head bobs 1 and 5 were at the top arm of the right 'T', and head bob 2 at the top of the left 'T'. These bobs were more like flicks, so quickly and precisely were they executed. An entire set was delivered in 1,2 to 1,4 ($\bar{x}$ = 1,35 sec) seconds. Four sets constituted a threat series, with 1,5 to 1,7 seconds intervals between each, and 1,9 to 2,2 seconds intervals between each series. Refusal of the transgressor to leave resulted in fight in *C. pumilus* in the field and in several observations vicious attacks resulted when the transgressor refused to acknowledge the defender's display. Frequently, they fell from trees with interlocked jaws. No deaths resulted, as in *C. namaquensis*, but severe injuries were incurred. As with *C. namaquensis*, females were more aggressive than males.

C. namaquensis territorial display consisted of lateral body compression, a stiff-legged erect stance, gorged throat (displaying purple interstitial skin) and partly gaping mouth, either Colour Index '5', excitement pattern (Hoesch's 'schreckmuster'), or in combination. In delivery, the combatants 'faced-off', with much hissing, head-bobbing, and weaving of the whole fore part of the body side-to-side, up and down; the rear was virtually stable, except in especially heated displays. Looking head on, the head-bobbing was laterally in the horizontal plane, describing an 'S' lying on its side, with the first and last bobs being delivered on the right. Five such bobs constituted a set (delivered in 2,8 sec), two to three sets per display with a one second interval between each. Refusal of the transgressor to leave the defender's presence resulted in combat, in which severe, often fatal, injuries were incurred. There was no 'submissive posture'; only flight of the transgressor averted a fight. Two patrolling *C. namaquensis* often displayed from their respective sides of a common border along its entire length.

A discussion of the literature in respect and synthesis of social interactions and display is included with that on territories.

4. *Size and structure of territories*

Chamaeleo pumilus had an undefended, shifting, vertical home range, with a vigorously defended night-time rest area. Shifting occurred only if the home range did not provide adequate food throughout the year. *C. pumilus* frequently walked considerable distances to locate new food sources. In plan view the home range area was about 10 m^2 in both sexes, but since it was at several different horizontal levels, or 'multi-storied', the actual area was much more. For example, *C. pumilus* occupying a bush 3 m high and of 10 m^2 in plan view with 20 such multi-storied plan areas, the actual home range area was about 600 m^2. It is, therefore, a more effective use of space. Juvenile *C. pumilus* had no sleeping area that they regularly used for a long time, and a continuously shifting home range.

For simplicity territories occurring in various biotopes and habitats have been placed under the type in which a given territory has most of its area. Such territories embracing different biotopes or habitats were considerably larger than most of those that were limited to one. Territory data are summarized in Table 32 and given in detail of biotope and/or habitat in Table 33. Maximum individual territories occurred in November for coastal males (8 000 m^2), females (1 632 m^2), inland males (1 752 m^2), and females (998 m^2), but mean territory sizes were largest in April (male; 2 429,0 m^2; female; 885,7 m^2—coastal only). One would suspect this to be true for inland populations, but insufficient data are available, thus, the maximum mean (1 435,7 m^2) of inland male territories was in June, and females (881,8 m^2) in November. Territories appeared to vary in size according to reproductive demands, that is, male territories generally increased in area during courting and those of females were enlarged during egg-laying.

Table 32

Summary of seasonal variation in territory sizes (in square metres) in coastal and inland populations of *Chamaeleo namaquensis* in South West Africa. Means are in parentheses. (For a detailed consideration by biotope and habitat, see Table 33.)

	N	Coastal	N	Inland
Feb.				
♂♂	16	771–6 800 (1 294,8)	4	1 109–1 300 (1 225,2)
♀♀	18	177– 800 (252,6)	6	790– 899 (858,0)
Apr.				
♂♂	21	800–7 200 (2 429,0)	0	—
♀♀	24	120–1 100 (885,7)	0	—
June				
♂♂	23	1 030–2 666 (1 192,1)	3	1 256–1 751 (1 435,7)
♀♀	15	101– 250 (176,5)	3	800– 920 (864,0)
Nov.				
♂♂	21	927–8 000 (1 954,1)	11	1 211–1 752 (1 089,6)
♀♀	17	102–1 632 (213,0)	8	700– 998 (881,8)

Table 33

Variation in territory sizes (in square metres) according to biotopes, habitats and season in coastal and inland populations of adult *Chamaeleo namaquensis*. Means are in parentheses.

	Dunes				River bottom			
	N	Coastal	N	Inland	N	Coastal	N	Inland
Feb.								
♂♂	0	—	2	1 236–1 246 (1 241)	6	872–1 010 (962)	1	1 109
♀♀	0	—	1	890	5	231– 250 (237)	2	790– 800 (795)
Apr.								
♂♂	2	1 416–7 200 (4 308)	0	—	5	1 020–1 931 (1 665)	0	—
♀♀	4	500– 620 (570)	0	—	6	130–1 011 (284)	0	—
June								
♂♂	8	1 200–2 666 (1 846)	3	1 256–1 756 (1 436)	5	1 030–1 800 (1 566)	0	—
♀♀	0	—	3	800– 920 (864)	5	127– 230 (174)	0	—
Nov.								
♂♂	4	1 632–3 264 (2 380)	3	1 252–1 752 (1 435)	5	1 030–1 800 (1 436)	5	1 211–1 331 (1 266)
♀♀	3	408– 816 (611)	0	—	5	132– 150 (142)	3	700– 800 (759)

	Gravel plain		Hummocks			
				River		Dune
		Inland (only)		Coastal (only)		
	N		N		N	
Feb.						
♂♂	1	1 300	5	862–6 800 (2 075)	5	771–1 412 (915)
♀♀	3	879– 899 (889)	9	177– 800 (263)	4	237– 280 (252)
Apr.						
♂♂	0	—	9	801–1 015 (874)	5	800–4 121 (1 540)
♀♀	0	—	10	120–1 000 (256)	4	200–1 100 (463)
June						
♂♂	0	—	6	1 232–1 601 (1 491)	4	1 200–1 600 (1 470)
♀♀	0	—	7	101– 240 (156)	3	210– 250 (230)
Nov.						
♂♂	3	1 229–1 311 (1 280)	8	927–8 000 (2 209)	4	1 532–1 800 (1 666)
♀♀	5	927– 998 (955)	6	102– 190 (152)	3	135–1 632 (667)

The territorial structure of *C. namaquensis* consisted of a more or less centrally located resting area, usually in a redoubt, but there were no surrounding areas of lesser or greater usage. On waking, chamaeleons patrolled to the border limits and encompassed their entire domain; as the day progressed they proceeded inwards in decreasing patrol courses towards the rest area and night-time retirement. In areas of micro-relief, such as hummocks, the border configuration closely followed the higher ground to an extent that a finger-like projection on such high ground of one chamaeleon's territory intruded into lowlands dominated by another. This system prevailed even on monotonously flat areas, and especially on dunes, where one would suspect territories to be circular, or squarish, since there was no local micro-relief to affect border configuration. There was no overlap of any territories with members of the same or the opposite sex. All ownership disputes, and most courting, were border incidents, and upon completion of courting the contact became a territorial challenge, the 'invading' sex partner being evicted. Usually the larger male territories were surrounded by female territories more than they bordered on those of other males. Female territories were smaller than those of males.

Juveniles had no territories of any discernible sort. They always slept on an object, not necessarily the same, and companionably together when the occasion warranted. Juvenile *C. namaquensis* occupied a shifting home range (10–53 m^2; $\bar{x} = 27{,}5$) that occurred wholly or partly in the strongly defended territories of the adults, from whom they were free of challenge. Recently hatched *C. namaquensis* initially had their home ranges within the territory of one of their parents, or within the territories of both parents. As they matured, the juveniles apparently began defending their home ranges as they stabilized their locations. By shifting an undefended space when juvenile and free of challenges, the young might find an unoccupied area that they can defend on adulthood.

Establishment of territories was impossible in captivity and this mediated an entirely different type of spatial occupancy in *C. pumilus* and *C. namaquensis.* Both defended favoured rest sites and *C. pumilus* giving birth and ovipositing *C. namaquensis* defended the parturition and nest site, respectively, from all intruders. Thus, in captivity both chamaeleons worked on a 'free run' basis, which, in the case of *C. pumilus* explains why previous authors considered it not to engage in fights, since they had not observed it in the field.

Literature accounts of lizard social organization are virtually limited to American forms, especially the iguanid *Uta stansburiana.* Harris (1964) studied social interactions in an agamid, and noted that female *Agama* in estrous are more submissive to males than non-estrous females. The same was noted in *Chamaeleo pumilus* and *C. namaquensis*, and by Fitch (1940) for *Sceloporus occidentalis*, Irwin (1965) for *Uta stansburiana*, *U. stejnegeri* and *U. hesperis* (Burrage 1966) and demonstrated (Ferguson 1966) as controlled in *Uta* by FSH.

Brain (1961) describes the display of *Chamaeleo dilepis* as similar to that of

C. namaquensis, but *C. dilepis* threatens broadside on, rather than in face-off position as in *C. namaquensis*. Bustard (1958: *C. jacksoni;* 1965: *C. hohnelii;* 1966: *C. bitaeniatus;* 1967: *C. gracilis*) describes the behaviour of several captive specimens, and in his discussion of *C. gracilis* also mentions observations on *Microsaura pumila* (= *Chamaeleo pumilus*) and *Chameleo chamaeleon* (= *Chamaeleo chamaeleon*). *C. jacksoni* exhibits ritualized fighting, using its horns to ward off attackers of its own and other species, and in intraspecific conflicts in attempts to dislodge each other. *C. hohnelii* possesses the most highly ritualized fight behaviour, with the use of more extreme colour changes of any other chamaeleon, the combatants circling each other with mock-biting, which settles encounters without injury. Schmidt & Inger (1965) describe display in *C. ituriensis;* submission is by assuming a drab colour, with which the wearer is safe from further attack. The male *C. hohnelii* is the more aggressive sex, with the reverse being true of *C. bitaeniatus*. *C. chamaeleon* and *C. gracilis* have threat display followed by actual fighting, inflicting severe, sometimes fatal, injuries, as is true of *C. namaquensis* and *C. pumilus* in the field. *C. gracilis* has a submissive posture, which secures the chamaeleon assuming it from attack from even an irate individual. In this posture the body is longitudinally extended making the minimal distance between dorsal and ventral areas. Both sexes of *C. pumilus* were observed to threaten other lizards, as Bustard (1965) notes for female *C. hohnelii*. Lateral compression, throat gorging, open-mouthed hissing and aposematic colour and patterns are the norm of chamaeleon display. In especially intense displays, they rock vigorously from side to side. *C. bitaeniatus* (Bustard 1966) and *C. pumilus* (Bustard 1967*a*) males do not fight and are less aggressive than the females. Bustard's observations as to display and behaviour patterns of *C. pumilus* are essentially as in this study and in most respects as found by Spence (1966) for *Microsaura damarana* (= *Chamaeleo pumilus*) and Von Frisch (1962) for *Microsaurus pumilus* (= *Chamaeleo pumilus*), except Von Frisch considers females less hostile than the males. Unfortunately, all these workers examined *C. pumilus* in captivity, whereas individuals of this species did give combat in the field.

Fighting in wild populations of lizards is rare, but has been recorded for the iguanids *Sceloporus grammicus* (Evans 1946) and *Uta stansburiana* (Burrage 1966; Tinkle 1967). There is no study, other than the results reported here, for *Chamaeleo namaquensis* and *C. pumilus*, on the significance of head-bobbing in chamaeleons at the level of Carpenter's (1962) and Hunsaker's (1962) investigation of the function of this in iguanids. Bustard (1966) found courting male *C. bitaeniatus* jerk the head. The head-bobbing display of *C. namaquensis* bears a close similarity to that which the author observed in the iguanid *Cyclura cornuta*.

Discussions of spatial occupancy in lizards are disconcerting, because of the varied techniques employed, consideration of widely separate populations in different habitats, physical factors, such as varied geologic substrates, local topography, and other biotic dynamics, for example, the population density of the studied species, plant density, and competitors. Also, despite the call for metrication, a not inconsiderable number of recent papers persist in utilizing outdated units, requiring tedious conversion and a double set of figures in any presentation reviewing data. With few exceptions, no attempt has been made to study adjacent populations in the same general area under slightly different conditions of local topography, geologic substrates, plant, and population density. For example, for five years in Southern California Burrage (1966) observed proximal coastal bluffs, sandy and rocky beaches, coastal and inland canyons, areas of rugged and flat topography and varied geologic substrates, plant density, and population density in an investigation of spatial occupancy of *Uta stansburiana hesperis* and found widely different territory sizes and social organizations obtaining at each study station. Jorgensen & Tanner (1963) used the density probability function obtaining larger territory sizes for this species in Nevada, than did Tinkle, McGregor & Dana (1962) using the minimum polygon method for this species in Texas. Furthermore, in Texas, *Uta* concentrates its activity around wood rat (*Neotoma*) nests in mesquite (*Prosopis*)—a rich source of arthropod prey—and, has less need to wander for food than those in Nevada. Thus, environmental factors in widely separated areas or adjacent areas of varied topography could account for an actual difference in territory size, rather than computation error.

Furthermore, as Tinkle (1967) observes, there are few studies based on large numbers of captures. Indeed, a lack of sufficient minimum recaptures is why no territorial data in April for inland *Chamaeleo namaquensis* are presented here. Most studies demonstrating territorial behaviour in lizards are based on temperate iguanids, with little speculation as to its adaptive significance in reptiles, as has been done by Nice (1941), Hinde (1956) and Carpenter (1958) for other animals, mostly birds. Rand (1967) has made a step in this direction, based largely on his observations of the iguanid *Anolis lineatopus* in Jamaica. Hypothetical values of territory can be: (1) securing a requisite share of environmental resources, and/or (2) mating, and/or (3) survival of the offspring. Rand reports that critical environmental resources for *A. lineatopus* need be defended intra- and interspecifically. In *Chamaeleo pumilus* and *C. namaquensis* food was certainly not critical, especially for the latter. *C. pumilus* defended only its favourite perch for sunning and rest, thus, a secure night-time shelter was critical to this species. The fact that *C. pumilus* was frequently found on top of grass stems in grassy areas away from shrubs cannot be assigned to a surplus, displaced population away from supposed 'choice' shrubs, because wild *C. pumilus* preferred reeds. The high metabolic rate of *C. namaquensis* may require spacing—as their rigid territorialism invokes—for more efficient exploitation of prey. Since *C. namaquensis* has ubiquitous habitat preferences, site selection cannot be important. Vigorous territorial defence for food by male and female *C. namaquensis* seems interesting, particularly when pugnacious defence of territories by both sexes in some lizards (e.g. *Sceloporus merriami*) occurs if food is the limiting resource (Milstead 1961). The structure of territories is possibly most valuable to *C. namaquensis*, for even if transgression was allowed in courting, it assured that any given male would meet more females than other males during the normal diel patrol of both sexes. Only captives defended the immediate nest site, and such defence must be considered an artifact of captivity. Since suitable nest sites were available in each female's territory, territorial defence in the field would limit or eliminate intrusion of the nest site *per se*. Defence of the nest sites and their location within the female territory prevented exhumation of buried eggs by other females digging a nest.

Bourgat (1968*a*) notes that each individual *C. pardalis* patrolled an area of several 10 square metres. There are no other comments of territory size in chamaeleons, but defence of a favoured perch is noted for *C. dilepis* (Brain 1961), *C. jacksoni* (Bustard 1958), *C. hohnelii* (Bustard 1965), *C. bitaeniatus* (Bustard 1966), *C. gracilis* (Bustard 1967*a*), and synonomies of *C. pumilus*, *Microsaurus pumilus* (Von Frisch 1962), *Microsaura pumila* (Bustard 1967*a*) and *Microsaura damarana* (Spence 1966). All these observations are based on captives, except those of Brain and Spence. Table 34 gives the mean territory and home range sizes of some lizards that are available in the literature. These data used the minimum polygon technique, or planimetry. It is important to an interpretation of chamaeleon home ranges to realize that most chamaeleons are aboreal, whereas the majority of the lizards investigated are terrestrial. Burrage (1966) notes that only the resting site is defended by *Uta stansburiana hesperis* in populations so large (>250 per acre; about >625,0 per hectare) that individual territorial establishment is impossible or unnecessary. In a consideration of territories of *Uta*, Burrage (1966) discusses at length the influence of intricately eroded and/or steep slopes in allowing the establishment of rather large territories in high population densities, which perhaps approaches the spatial relationships of *Chamaeleo pumilus*. This paper also considers local topography, relief, and slope angle, differences in geologic substrates, plant density, and lizard population density at coastal and inland sites in a small geographic area to assess factors regulating the establishment of territories and social organizations in *Uta stansburiana hesperis*.

Knowledge of social behaviour in reptiles is poor; what is known is somewhat confusing, since display patterns appear in newly hatched or newborn young, as observed in *Chamaeleo pumilus*. Carpenter (1967) gives an interesting review of social behaviour of iguanids, with pertinent references, and a detailed study (Carpenter 1961) of social behaviour of the desert iguana *Dipsosaurus dorsalis*. Hunsaker & Burrage (1969) studied a multi-species assemblage of captive iguanids and demonstrated a shift from territories to a social hierarchy as a result of population pressure and reduction of available area. This hierarchical system is established by increasingly vicious fighting, rather than the normal displays, as population pressure increases, and/or the available area is reduced. Similar social hierarchies in wild populations of normally territorial iguanids are noted for *Ctenosaura pectinata* (Evans 1951). Burrage (1966) studied the various social relationships of *Uta stansburiana hesperis* of California in relation to habitat and physical factors, population

Table 34

Review of mean territory and home range sizes of some of the lizards reported in the literature.

			Area occupied			
Species	Sex/Age		Acres	Metres^2	Remarks	Source
Amblyrhynchus cristatus	♂♂	ad't.	—	1,0	only in breeding season	Carpenter (1967)
	♀♀	,,	—	—	only displays	,,
Ameiva quadrilineata	♂♂	juv.	—	16,4		Hirth (1963)
	♀♀	,,	—	15,1		,,
	♂♂	ad't.	—	21,1		,,
	♀♀	,,	—	13,7		,,
Anolis sagrei	♂♂	,,	—	>36,0		Evans (1938)
Basiliscus vittatus	♂♂	juv.	—	14,9		Hirth (1963)
	♀♀	,,	—	12,4		,,
	♂♂	ad't.	—	12,0		,,
	♀♀	,,	—	12,2		,,
Chamaeleo namaquensis	♂♂+♀♀	juv.	—	27,5		this study
	♂♂	ad't.	—	1 717,5	coastal	,,
	♂♂	,,	—	1 250,2	inland	,,
	♀♀	,,	—	382,0	coastal	,,
	♀♀	,,	—	867,9	inland	,,
Chamaeleo pardalis	♂♂+♀♀	,,	'several 10 m^2'			Bourgat (1968*a*)
Chamaeleo pumilus	♂♂+♀♀	,,	—	600,0		this study
Cnemidophorus hyperythrus	♂♂	,,	0,07	283,3		Bostic (1964)
	♀♀	,,	0,10	404,7		,,
Cnemidophorus tigris	♂♂+♀♀	juv.	0,09	364,2		Jorgensen & Tanner (1963)
	♂♂	ad't.	0,50	2 023,5		
	♀♀	,,	0,24	971,3		,,
Ctenosaura pectinata	♂♂+♀♀	ad't.	—	2,1		Evans (1951)
Sceloporus olivaceus	♂♂	juv.	0,027	109,3		Blair (1960)
	♀♀	,,	0,017	68,8		,,
	♂♂	ad't.	0,17	687,9		,,
	♀♀	,,	0,07	283,3		,,
Uta stansburiana hesperis	♂♂	juv.	0,005	20,2	California	Burrage (1966)
	♀♀	,,	0,004	16,2	,,	,,
	♂♂	ad't.	0,05	202,4	Calif. coastal	,,
	♀♀	,,	0,034	137,6	,,	,,
Uta stansburiana hesperis	♂♂	ad't.	0,075	303,4	Calif. inland	Burrage (1966)
	♀♀	,,	0,056	226,6	,,	,,
	♂♂	,,	0,021	85,0	intertidal home range of strand-dwellers	,,
	♀♀	,,	0,016	64,8		,,
Uta stansburiana stansburiana	♂♂+♀♀	juv.	0,04	161,9	Nevada	Jorgensen & Tanner (1963)
	♂♂	ad't.	0,10	404,7	,,	
	♀♀	,,	0,03	121,4	,,	,,
Uta stansburiana stejnegeri	♂♂	,,	0,11	445,2	Texas	Tinkle (1967)
	♀♀	,,	0,03	121,4	,,	,,

pressure and food supply. The social organization of other races of *U. stansburiana* have been studied by Tinkle (1967). Clarke (1965) studied several iguanids in captivity, showing formation of dominants–sub-dominants hierarchies. Harris (1964) gives a detailed account of social behaviour in the agamid, *Agama agama*, noting formation of social hierarchies in high population densities. Harris further notes the establishment of territorial borders in *A. agama*, where two males fought several times over a path between their boundaries. Fighting decreased and eventually display along the path replaced combat as the border became established, with rare attempts at violation. Establishment of social hierarchies in high population densities limits the frequency of antagonistic behaviour that would result in attempts at territory formation. This has been demonstrated by Soulè (1964) and Burrage (1966) in the case of littoral and insular high density populations of *Uta*, where only the retreat burrow of each lizard is defended and only a 'free run' home range exists. This has also been noted by the latter author for some inland populations and is always associated with abundant food supplies.

K. *Reproduction*

1. *Sex determination and description of adult Chamaeleo pumilus and C. namaquensis*

Males are the smaller sex in *C. namaquensis* and *C. pumilus*. Male *C. pumilus* have a slightly longer tail length (49–56%; x̄ = 53% of total length) than females (39–56%; x̄ = 47%). In *C. namaquensis* the tail length never exceeds the snout-vent measurement and tail length as a percentage of total length is nearly equivalent in the sexes (males; 30–44%; x̄ = 38%: females; 23–50%; x̄ = 38%). In both species the limb proportions are more robust in males, especially the hind, and the head proportionately larger, more rugose and ornamented as compared with females. The tail base of males, housing the paired copulatory organs, is larger and has a distinctly swollen appearance when the animal is reproductively active. The hemipenes can be everted by gentle pressure on the tail base to determine sex at any age.

Zoond & Eyre (1934) describe the general pattern of *C. pumilus* to consist of stripes, patches and individually coloured skin tubercles, arranged as 'bands' (mid-laterum), 'islands' (large tubercles within the bands), 'margins' (dorsal and ventral to the islands), and 'back' (area dorsad of the margins). Bands are always present, though varying in width and distinctness between individuals, and at thermal neutrality (Colour Index '2–3') are orange or brown. The ground colour of the back in adults is usually green, though some have it brown, russet, or yellowish at thermal neutrality, which is essentially a continuation of a juvenile colour type (Table 48). In these individuals, always females, brown predominates and there is really no distinct pattern. The usually blue or gray islands and margins vary and may be totally absent in some, especially females. The margins are quite wide and often intensely bright blue in some males. Some *C. pumilus* have large orange tubercles in the back, or green region. Further discussion of the pattern of *C. pumilus* is given by Zoond &

Eyre (1934) and as they note, it is extremely variable with individuals, and changes somewhat in each through the Colour Index, since each colour, and thus the pattern lay out, is masked, or enhanced through the values of the Colour Index. However, a brown one, for example, cannot go green, or vice versa, but only 'light' or 'dark' phases of these colours; a feat also noted by Farghaly (1941) for *C. vulgaris* (= *C. chamaeleon*) and a host of others back to Aristotle.

The 65 male *C. pumilus* examined varied in snout-vent from 53,0–93,0 mm (x̄ = 73,5 mm), with the tail 55,5–107,0 mm (x̄ = 82,3 mm). The 86 female *C. pumilus* examined had a snout-vent length of 51,0–102,0 mm (x̄ = 78,8 mm), with the tail 52,0–103,0 mm (x̄ = 78,0 mm). Spence (1966) collected 4 males and 7 females of *Microsaura damarana* (= *C. pumilus*) at the Storms River bridge in the Tsitsikama National Park, Cape Province. He found the snout-vent length to be 54,6–78,0 mm (x̄ = 62,9 mm) in the males; and that of the females to be 51,6–78,3 mm (x̄ = 65,8 mm). Tail length for the Tsitsikama males ranged from 125,2–192,5 mm (x̄ = 147,7 mm), with the tail 55,4–59,5% (x̄ = 57,2%) of the total length, and for the females tail length ranged from 58,5–97,5 mm (x̄ = 77,0 mm), with the tail 50,9–55,5% (x̄ = 53,6%) of the total length. Since (see pp. 6–7) this study follows Hillenius (1959), it is not known whether the differences in sizes and the tail as a percentage of the total length between Spence's Tsiksikama *M. damarana* (= *C. pumilus*) and *C. pumilus* in the southern Cape Province are ascribable to his smaller sample (i.e. random error), genuine specific, or subspecific differences, or simply a geographic cline within a species. Bustard (1966) noted that the sexes of the viviparous chamaeleons rest differently; the males longitudinally stretched, with the tail straight out; the females hunched, with the tail in an ungripping coiled watch spring.

There are no sexual, or age pattern differences in *Chamaeleo namaquensis*, but there are differences in pattern (Table 35) and proportions between coastal and inland individuals. For example, the depth and breadth of the head of most coastal specimens are almost equal and the body stockier and more porcine, while most inland individuals have a conspicuously long, deep,

Table 35

The percentage of ground colour types in the inland and coastal populations of *Chamaeleo namaquensis* (coastal N = 100; inland N = 40).

Ground colour type	Populations						
	Inland			Coastal			
	Dunes	River bottom	Gravel plain	Shore	Dunes ±8 km in	River bottom	Gravel plain
Sulphur yellow	—	—	—	80	35	10	2
Reddish	87	15	—	—	15	—	—
Gray	13	85	100	19	20	50	97
Green	—	—	—	1	30	40	1

narrow skull, and the body form and proportions are more attenuated and slender. The tail length as a percentage of the total length also differs.

2. *Courting*

Courtship was observed in the field and captivity during all months except June and July in *Chamaeleo pumilus* and from April to July in *C. namaquensis*. It is similar in pattern to that described for the African *C. dilepis* (Cott 1934), Trench (1912) for the Indian *C. calcaratus* (= *C. chamaeleon zeylanicus*) and *C. vulgaris* (= *C. chamaeleon*) as described by Schrieber (1912).

C. pumilus courted only in bushes. Courting *C. pumilus* males are a bright green, the females usually dark. In most respects as to head and body motions the courtship of *C. pumilus* closely resembles that given below for *C. namaquensis*, except the former head bobs more jerkily in a flat, horizontal plane. In *C. pumilus* the tail is kept on the branch and there is no circling dance. Presumably this is because courtship occurs in different situations in the two species. Coitus is as described below for *C. namaquensis* and in *C. pumilus* lasts from seven to fourteen minutes. Bustard (1963) observed courting in *Microsaura ventralis* (= *C. pumilus*), with coition lasting up to two hours. Von Frisch (1962) found *Microsaurus pumilus* (= *C. pumilus*) copulated for eleven minutes. During coition the female is passive, but becomes aggressive after coitus, which temperament lasts until termination of her pregnancy. As also observed in the literature cited here on chamaeleon breeding, these animals are solitary, tolerating close proximity only during mating. *C. pumilus* and *C. namaquensis* were seen to copulate two to three times per day, several times per week, and both sexes are even more aggressive to members of their own sex (see population structure p. 105) at such times.

Courting *C. namaquensis* of both sexes are mottled and spotty. The male *C. namaquensis* approaches the female with his tail held up and commences 'dancing' around her with a slow, pronounced weaving side to side of the body; not fast as with the territorial challenge. This is similar to head-bobbing in other lizards, but in *C. namaquensis* the body and head bob in unison, as it were. However, the head concurrently describes a horizontal 'S'-shaped bobbing in challenge, which may evidence itself in initiation of courtship (see p. 101). The large female, if receptive, remains passive, or 'face-offs' the male. Then he intensifies his display with sideways jerks of the head and exaggerates his highly erect 'dancing' stance, lateral body compression, and tail held high. Continuing, both open their mouths and 'bisss' at each other, lunging, weaving back and forth, and flicking their tails at each other. If the male touches the female, she may feign biting, but usually prods him with her jaws closed. At the onset of copulation the female bolts a short distance, pursued by the male. The female halts in a highly erect and exaggerated stance, and the male climbs on to her back just anterior to her hind legs, his hind limbs gripping hers on their dorsal surfaces. The plantar surface of the male's fore paws are placed on the front of the female's axilla. The male swings down his tail under the female's tail base, bringing their vents in apposition. One of the hemipenes is everted and enters the female's cloaca. Copulation lasts for five to fifteen minutes in 'adpressed' Body Compression 'I' and is of the normal saurian pattern.

Sex recognition is by sight in the related iguanids and agamids, and in these, differences in colour, shape and behaviour are used in sex determination. Since size is the only unvarying difference in the chamaeleons studied, it is difficult to know whether this would have any value in sex determination for a large male and a small, recently matured female, or one medium-sized. Mating in chamaeleons may start off as a challenge and the answering behaviour of the female to this determines the outcome. Brain (1961) considered there were frequent rebuffs to homosexual mating attempts due to 'mistakes', with the enraged and unwilling male partner pulling off his attacker. This may be so for the *C. dilepis* Brain observed, but in *C. pumilus* and *C. namaquensis* such injuries were due more to territorial fighting and in these species both sexes had such back scars. Non-receptive females aggressively asserted themselves by biting the inguinal region and flanks of a potential suitor, and since the females are larger than the males, this frequently ended in damaging injuries and death. This occurrence is particularly true in *C. namaquensis.*

Trench (1912) observed copulating *C. chamaeleon zeylanicus* in October, noting mated females were a jet black and aggressive to males. Bons & Bons (1960) say courting occurs in August and September in the North African deserticulous *C. chamaeleon.* Brain (1961) gives a four month gestation period for the East African *C. dilepis,* putting courtship back to about May, agreeing with Milner (1947). Cott (1934) observed *C. dilepis* courting in February in Mozambique.

Only recently ovulated females of *C. pumilus* and *C. namaquensis* were receptive to males, a condition noted in iguanids by Burrage (1966) for *Uta stansburiana hesperis* and *Sceloporus occidentalis* (Fitch 1940).

3. *Description of the eggs of Chamaeleo namaquensis*

Fresh-laid eggs were beige, becoming immaculate white with thin, parchment-like shells, though the sand usually adhering to them gave them a reddish appearance. Of 250 *C. namaquensis* eggs examined (Table 36) in the field and captivity, the largest was 26,0 × 14,5 mm, 2,8 g; the smallest 17,5 × 10,0 mm, 1,2 g ($\bar{x}$ = 20,5 × 11,6 mm; 1,5 g). FitzSimons (1943) states that *C. namaquensis* eggs average 20 × 13 mm at laying. *C. dilepis* eggs may be spherical (diameter 8,0–10,0 mm (FitzSimons 1943), 12,5 mm (Wager 1958)) or oval (12,0–16,0 × 7,0–8,0 mm (FitzSimons 1943), 10,8–15,4 × 7,2–10,6 mm (Brain 1961)). *C. gracilis* eggs when laid average 10,0 × 14,0 mm (Menzies 1958), and Shaw (1960) gives *C. basiliscus* eggs as being 10,0–14,8 × 9,5–13,5 mm, 0,7 g ($\bar{x}$ = 13,3 × 9,9 mm; 0,67 g). All in all, there is a dearth of information on chamaeleon eggs as compared with other saurians.

Table 36

Monthly egg-laying data for *Chamaeleo namaquensis* showing size and weights of females before laying their eggs, size and weights of eggs at oviposition, and numbers and size of clutches. Dimensions are in millimetres and weights in grams. 'S-V' denotes snout-vent.

Month	Size of females s-v	+ tail	Weight	s-v+tail		Wt	N	Clutches size range	x̄	Size of eggs length	+ width	Weight	l×w		Wt
	Ranges			Means						Ranges			Means		
May . . .	106–141	77–86	55– 86	121	84	65,9	4	10–15	12,5	18,5–22,0	10,0–12,5	1,2–1,7	20,0	11,5	1,5
June . . .	106–120	64–96	55– 65	114	81	58,6	4	12–13	12,5	19,8–21,0	11,0–12,8	1,5–1,7	20,3	12,0	1,6
July . . .	115–140	78–96	51–155	135	89	82,4	4	10–22	13,0	18,0–21,0	11,5–13,5	1,4–1,7	19,7	12,5	1,6
Aug. . . .	108–115	71–96	55– 82	111	84	65,6	3	10–12	11,7	17,5–24,0	10,0–14,5	1,2–2,8	19,6	11,6	1,7
Sep. . . .	90–143	72–86	60–100	121	81	77,7	4	6–13	9,5	18,0–26,0	10,0–13,0	1,2–1,9	21,4	11,3	1,5

4. *Parturition sites of Chameleo pumilus and nesting sites of Chameleo namaquensis*

Chamaeleo pumilus females giving birth select small-leaved shrubs or grass stems. Parturition of 56 litters for a total of 614 young was observed. In any given litter, time between births of young took less than a second to as much as 13 minutes ($\bar{x}$ = 8 min, 10 sec). The time between parturition and the young being active and free of their membranes was usually immediate. About 10% were born internally, appearing free of their egg membranes and exhausted yolk sacs, which came out first. The entire birth process may take nearly two hours for a litter complement of 10 or more young, or as little as twenty minutes for a litter complement of 5 or less. Abel (1931) found *C. pumilus* and *C. melanocephala* (= *C. pumilus*) to give birth to nine young in one and a quarter hours. Bustard (1955, 1965, 1966) records and compares birth in several viviparous chamaeleons, including *C. bitaeniatus*, *C. hohnelii*, *Microsaura pumila* and *M. ventralis* (= *Chamaeleo pumilus*). Nine *Chamaeleo pumilus* young freed themselves and were active in a minute, six *C. bitaeniatus* were free in 1,3 minutes, but *C. hohnelii* took 5,3 minutes. Bustard (1955) gives the entire birth process of seven *C. pumilus* as lasting 24 minutes, with the average time of the birth process of individual young as 1 minute, 42 seconds (range: 0,15 sec to 4 min) and the average time between births of individual young as 2 minutes, 50 seconds (range: 0,04 sec to 7 minutes, 15 seconds).

Chamaeleo namaquensis nests were constructed in the typical oviparous chamaeleon manner, consisting essentially of a hole large enough for the female with a terminal enlargement for her to turn around in at the end of excavation and commencement of egg-laying. In the field favoured nest sites were loose gravel, and especially the foot of and the windward slopes of large dunes, and below the crest of small (6 m high) ones. Such sites were abundant in the field, and each female had its own nesting site located within its tightly defended territory. In crowded, captive conditions an area 350 mm in diameter was viciously defended against intrusion by other females, gravid or not, and even males. For up to a week prior to laying, most females dug exploratory holes to a depth of 130 mm; which, presumably, was in search of the layer of moist sand under which the eggs were laid. In captivity, the eggs were laid at 100 mm total depth, provided an artificial layer of saturated sand was available.

The construction of six nests in captivity for a total of 83 eggs was observed, and two nests in the field for a total of 25 eggs. Only data in Table 36 refer to the 225 eggs laid in captivity. Nest-building in captivity was as in the field, and the process was observed by inserting a horizontal glass viewing plate, under which the animals dug. Some completed nests were excavated to examine their form. After preliminary holes had been dug, the preferred site was selected, usually on a slight rise, since a steep slope would invite tunnel collapse in digging, especially through the initially dry, non-cohesive upper substrate layers. Nevertheless, the top portion of the nest was about 300 mm in diameter, plus a spoil heap of 1,20 m. The nest was constructed as a pit down to the loose, moist sand layer, which was 10 mm subsurface in gravel, deeper for dune sand, and extended for a depth of approximately 150 mm, becoming dry deeper than this. It was to this dry layer below the loose, moist layer that *C. namaquensis* dug. Excavation through the moist area was narrow (approximately 150 mm wide) and the terminal enlargement in the dry area beneath this was 77 mm or more, so that the nest had an appearance of a wide-mouthed, beakered flask, with a narrow neck and wide base. Dug at an angle of 60–80°, the nests were almost consistently of an overall depth of 200–250 mm, rarely more, never less. The female excavated this with her eyes closed by using her head as a battering ram, pushing vigorously forwards and laterally, and somewhat up and down. The right fore and left hind feet acted as braces, while the left fore foot dug, pushing the excavated spoil back to the right hind foot for evacuation. This arrangement was alternated back and forth in the course of excavation. As the spoil accumulated behind, the female cleared this by backing up and using the hind feet as ploughs until at least 350 mm clear of the excavation area, where the spoil was dumped on the heap. At the top of this heap, the female shook off the spoil that had accumulated on the top of her head, then opened her eyes and walked back to more excavating. Nest excavation occurred at any time of the day or night. The time from the start of excavation to completion of oviposition took as little as eight or as long as ten hours, with no rest between excavation and oviposition.

The first eggs were laid with the female facing tail outward, positioning the dropped eggs with her fore feet as they rolled from her cloaca under her body and down to the terminal enlargement. In ovipositing the tail was held up as space permitted, the pelvis resting on the floor, and the legs held high and far apart, especially the hind ones. Passage of eggs resembled defecation. Six to eight eggs were well-spaced in the loosened floor of the terminal enlargement and constituted the first layer of eggs, which was then covered by spoil and then another layer of eggs and so on. As the terminal enlargement filled, the female reversed her position and with the head then pointing outward completed egg-laying, each egg layer being separated from that above and below it by a layer of spoil. The final layers were positioned with the hind legs, and the upper spoil layer tamped down. The first eggs were laid at average intervals of 20 minutes, which became progressively shorter as laying proceeded. At mid-laying the interval between eggs averaged 10 minutes, 7 minutes towards the end, and to as little as 30 seconds or almost instantly for the last dropped. Depending on the clutch complement, one or two hours comprised the ovipositing period. Upon emerging at the conclusion of egg-laying, the female used her hind legs to push spoil back into the hole to fill it. This final operation proved interesting in captivity, since other *C. namaquensis* of both sexes sometimes assisted. Spent females ate to capacity and captives must be given as much food as desired.

Chamaeleo basiliscus (Shaw 1960), *C. chamaeleon zeylanicus* (Trench 1912), *C. dilepis* (FitzSimons 1943; Milner 1949; Wager 1958; Brain 1961) and *C. gracilis* (Menzies 1958) all construct nests as does *C. namaquensis*, except that those of *C. dilepis* are at a less steep angle (45°) and may be considerably deeper (250–700 mm), as those of *C. chamaeleon zeylanicus* (to 350 mm), or considerably shallower (85 mm) as those of *C. gracilis*. Digging time may be as much as 60 hours (*C. chamaeleon zeylanicus*), 44 hours (*C. gracilis*), or 24–30 hours (*C. dilepis*). Rain-moistened soil is selected for ease of digging in these species, and in the case of tropic forms construction of nests coincides with the end of the rainy season.

5. *Annual number and size of litters of Chamaeleo pumilus and clutches of C. namaquensis*

Sexually mature *C. pumilus* females had four litters per year; the size of the female bears some relation to litter size, and the larger females had the largest litters (Tables 29, 37, 38). The first litter (7–9; x̄ = 8) of newly matured females (snout-vent 51–60 mm) was larger (3,0–6,0; x̄ = 5,1) than that of those 61–70 mm snout-vent. Births have been recorded in February to May, September, November, and December. The largest litters (5,0–21,0; x̄ = 17,0 young) were born in December; the smallest in April (3,0–6,0; x̄ = 4,5), overall; 3,0–21,0 (x̄ = 11,0). The difference in size of the young, according to parturition month, is discussed later.

Table 37

Number of embryos and developing oviducal eggs per month in relation to the snout-vent length of female *Chamaeleo pumilus*. (Means are in parentheses.)

	Snout-vent length in millimetres					
Month	51–60	61–70	71–80	81–90	91–100	101–110
Feb.	7		8–13 (10,5)	11–16 (13,5)	18	
Mar.		3–5 (4,6)	11	6–15 (13,3)		
June			18	21		
July			13	7–18 (12,5)	12–13 (12,5)	17
Aug.			12	12		
Sept.		6	7–10 (8,5)	18		
Oct.	9		11–16 (13,5)		19	
Dec.			10–11 (10,5)	14		
Jan.		5	11	10		

Table 36 gives the size of female *Chamaeleo namaquensis*, the size of clutches laid by each, and all other pertinent data. *C. namaquensis* eggs have been recorded from May to September. Regardless of the size of the laying female, the clutch complement was largest in those laid in July (10,0–22,0; x̄ = 13,0) and smallest in those of September (6,0–13,0; x̄ = 9,5). The majority of those laying in September were recently matured females, though considerably larger and older females laid the same number (Table 39). The overall clutch complement was 6,0–22,0 (x̄ = 13,2). September clutch eggs were slightly larger (18,0–26,0 × 10,0–13,0 mm; 1,2–1,9 g; x̄ = 21,4 × 11,3 mm; 1,5 g) than those of other months (Table 36). Females laid two to three, possibly four clutches per year (Tables 30, 40).

Table 38

Monthly birth data for *Chamaeleo pumilus* showing pre-parturition size and weights of females, offspring size and weights at parturition, and litter complements. Sizes given in millimetres; weights in grams. (See Table 46 for pattern and sex analyses of newly born young.)

	Size of females						Litters			Size of offspring					
	s-v+tail		Wt.	s-v+tail		Wt.		Size		s-v+tail		Wt.	s-v+tail		Wt.
Month	Ranges			Means			N	Range	x̄	Ranges			Means		
Feb.	51–99	52–97	7,4–22,5	78,7	73,5	16,3	12	5–18	11,8	20–24	22–27	0,3–0,5	22,0	24,5	0,4
Mar.	70–87	65–91	9,4–17,6	81,2	79,4	14,3	14	5–15	9,7	19–24	19–22	0,2–0,4	21,8	21,1	0,3
Apr.	51–62	52–64	5,0–10,0	56,5	58,0	7,5	4	3– 6	4,5	20–24	23–26	0,3–0,4	22,0	24,0	0,4
May	53–70	58–84	6,2–14,0	67,7	69,3	9,8	6	3– 9	6,0	19–24	19–23	0,2–0,4	22,0	21,6	0,3
Sept.	75–77	80–83	17,5–22,0	76,0	81,5	20,8	6	14–15	14,3	17–26	16–26	0,2–0,5	20,5	19,8	0,32
Nov.	76–80	80–84	19,0–22,0	77,7	82,0	20,3	8	8–16	11,8	22–27	20–26	0,3–0,4	24,7	23,9	0,35
Dec.	50–99	51–97	8,0–24,0	70,3	80,0	15,0	6	5–21	17,0	20–24	22–27	0,3–0,5	22,0	24,5	0,4

FitzSimons (1943) gives a clutch size of 20 eggs for *Chamaeleo namaquensis*. Clutch size in other oviparous chamaeleons varies from 10 in *C. chamaeleon zeylanicus* (Minton 1966) and *C. dilepis* (Brain 1961) to as many as 31 in *C. chamaeleon zeylanicus* (Trench 1912) and 45 in *C. gracilis* (Menzies 1958), and as high as 57 in *C. dilepis* (Wager 1958). The average clutch complement of oviparous chamaeleons is 30–40.

Table 39

The monthly number of oviducal eggs and yolked ovarian follicles at or greater than five millimetres in diameter in relation to the snout-vent length of female *Chamaeleo namaquensis*. Means are in parentheses.

	Snout-vent length in millimetres					
	81–90	91–100	101–110	111–120	121–130	131–140
Apr.						
Oviducal eggs	5			13		
Ovarian						3
June						
Oviducal eggs			10			
Ovarian			14	2	11	
Aug.						
Oviducal eggs			10			
Ovarian			14	2	12	
Nov.						
Oviducal eggs						
Ovarian	7			2	8–13 (10,5)	
Feb.						
Oviducal eggs						
Ovarian	10	20	15			25

Table 40

The growth and reproductive states in captivity of five male and five female *Chamaeleo namaquensis*. Dimensions are in millimetres; weights in grams.

	April				August				November			
Sex	s-v+tail		Wt	Rep.	s-v+tail		Wt	Rep.	s-v+tail		Wt	Rep.
♂♂	105	77	43	IBL	108	80	50	IBL	115	82	52	IBL
♂♂	97	84	37	IBL	101	88	42	IBL	112	100	51	IBL
♂♂	135	72	50	IBL	136	82	54	IBL	140	103	66	IBL
♂♂	120	70	45	IBL	123	73	47	IBL	130	75	54	IBL
♂♂	75	55	13	IBL	86	58	18	IBL	90	60	27	IBL
♀♀	108	90	50	GR	110	90	57	GR	110	90	62	LYF
♀♀	127	85	85	GR	132	71*	89	GR	135	72	113	GR
♀♀	117	83	70	GR	120	90	60	LYF	121	100	51	SYF
♀♀	86	85	47	GR	100	70	61	LYF	109	92	81	GR
♀♀	82	78	45	GR	98	80	40	SYF	101	89	49	LYF

* = Part of tail bitten off in a territorial dispute over an egg-laying site with another female.
s-v = snout-vent
Wt = weight
Rep. = reproductive state
IBL = in bloom (♂♂ only)
GR = gravid (oviducal eggs)
SYF = small yolked follicles (<5 mm diam.)
LYF = large yolked follicles (>5 mm diam.)

Oviparous chamaeleons lay far more eggs than saurians of comparative size or slightly larger (Mayhew 1968), including the closely related agamids. This prolificity is shared by viviparous chamaeleons. *C. pumilus* was found to have litter sizes as high as 21 young as did Spence (1966) for *Microsaura damarana* (= *C. pumilus*). Of viviparous chamaeleons, the overall average of young per litter is about 10, according to data from this study, Abel (1931), FitzSimons (1943), Atsatt (1953), Bustard (1955, 1963) and Von Frisch (1962). Three is the smallest recorded litter size, agreeing with this study. Angel (1933) records a maximum litter size of 20 for *C. leikipiensis* (= *hohnelii*), with an average of 12–13; and Bustard (1965) gives a litter size of 8,0–11,0 ($\bar{x} = 10{,}0$) for *C. hohnelii*. *C. bitaeniatus* has litters of 3,0–25,0 ($\bar{x} = 17{,}3$) young (Bustard 1966).

6. *Success of the litters of Chamaeleo pumilus and the clutches of Chamaeleo namaquensis*

Predation on eggs has never been recorded, but ants and burrowing insect larvae may be a potential threat to *Chamaeleo namaquensis* eggs. Some females did dig an extension to their retreat burrows for laying their eggs, and the continued presence of the adult in such instances might convey a measure of protection. Fitch (1956) felt the iguanid *Crotaphytus collaris* to suffer a high nest mortality with some potential clutches not being represented by any hatchling. In the field all the potential clutches of *Chamaeleo namaquensis* (Table 30) and the litters of *C. pumilus* (Table 29) were represented. In the case of *C. namaquensis* there appears to be evidence of a fourth clutch (Table 30). However, it is better to consider this (Table 30) the first clutch of newly matured individuals, since confirmation is lacking of any one marked female having four clutches a year.

Clutch and litter success are complexly intermeshed with such factors as weather, gestation, incubation, predation on gravid or pregnant females, growth of the recently hatched or newborn young, and availability of food for the young. In oviparous forms rainfall is very crucial to the success of certain clutches (cf. Burrage 1966, for the iguanid *Uta stansburiana hesperis*, and Mayhew 1968, for all desert saurians), as unseasonal rains seem to destroy nests or promote spoilage of the eggs, though, in fact, most desert saurian eggs quickly shrivel up in dry sand and need direct application of water, maintenance of 100% humidity being insufficient. However, nests of *U. s. hesperis* exhumed towards the end of incubation are quite dry, though moistness prevailed at laying and during early incubation. Thus, on a purely meteorological basis, the second and third clutches of this iguanid are the most likely to hatch. The *Chamaeleo namaquensis* observed inhabits an area of scant and erratic rainfall, though considerable moisture from fog condensate was closely associated with the eggs throughout the entire incubation period. It would be interesting to know the moisture relations of those eggs of *C. namaquensis* laid outside the fog belt.

7. *Role of fat bodies*

The work of Harris (1963) on the anatomy of *Agama agama* was applicable for use with chamaeleons. *Chamaeleo pumilus* and *C. namaquensis* have a four-lobed fat body, consisting of two small ventral and two large dorsal lobes, all connected at their posterior ends to the pelvis. Hahn & Tinkle (1965) demonstrated the role of these fat bodies in the ovarian follicle development of the iguanid *Uta stansburiana*. Their significance to the males, which are also subject to cyclical fat body changes, has not been investigated. Hahn & Tinkle showed that ovariectomy in *Uta* eliminated rapid lipid mobilization from the fat bodies, which occurred in those sham-operated. Fat body excision in early estrous *Uta* females induced a high incidence of follicular atresia, and retarded the yolk deposition rate. In pre-estrous *Uta* females follicular growth is delayed or inhibited by fat body excision. The extractable lipid in pre-estrous fat bodies is nearly equivalent to the lipid content in a typical clutch of eggs. Hahn & Tinkle concluded that the adaptive value of the fat bodies is associated with the formation of the first egg clutch, which is the most important.

Tables 41 and 42 for *Chamaeleo pumilus* males and females, respectively, and Tables 43 and 44 for *C. namaquensis* males and females, respectively, and Table 48 for juvenile *C. pumilus* and *C. namaquensis* show the fluctuation in fat bodies according to the reproductive state. It will be noted that in the males fat body size was greatest at those times the testes were active. In *C. namaquensis*, females with developing follicles had the largest fat bodies, and those reproductively quiescent or about to oviposit, the smallest. They follow the pattern of utas. Fat bodies were larger in female *C. pumilus* with embryos over 10 mm snout-vent and with yolking follicles, especially those in excess of 5 mm diameter. Thus, the fat bodies of *C. pumilus* would appear to have a dual role, lipid mobilization for follicle development, and possibly sustenance of the embryos in the later stages of pregnancy.

Fat body excision in four male *C. pumilus* and four male *C. namaquensis* resulted in a decline of testicular activity. Controls which had been sham-operated were unaffected. For four female *C. namaquensis* the results were as for female uta. In six female *C. pumilus*, results on follicular development were as for *C. namaquensis*, and in pregnant ones, only those with very late term foetuses (i.e., near birth) completed delivery of young. For the others, fat body excision resulted in the termination of pregnancy, abortion or resorbtion of the embryos.

It appears that fat storage in chamaeleons and utas is primarily for reproduction, whereas deserticulous gekkonids store sufficient caudal fat in four days of food ingestion to sustain them for up to nine months (Bustard 1967*c*).

8. *Nature of gonads* (*adult non-reproductive*)

Gonadal state was determined macroscopically and by microscopic examination of serial sections of organs. Inactive testes presented a flattish or squashed appearance externally, and internally the organ was somewhat transparent, as the epithelium of the tubules was thin and they were loosely convoluted. Sperm ducts not containing semen were thin, whitish to opaque, and wavy to moderately convoluted. Inactive males had a markedly less swollen tail base. In June and July *Chamaeleo pumilus* had inactive testes (Table 41), though in the former month semen was present in the distal part of the sperm duct. In July and August there was no semen in the distal part of the sperm duct, though in August 95% of the males had active testes. In *C. namaquensis* inactive testes were predominant (75%) only in August (Table 43), though all males sampled had semen in the distal part of the sperm duct.

9. *Nature of gonads* (*adult reproductive*)

Reproductively active testes occurred from August to May in *Chamaeleo pumilus*, and from February to April, June to August, and in November in *C. namaquensis* in the field and from April to November in captivity. These data suggest virtually reproductively active testes throughout the year in *C. namaquensis*, and it is probably the method of sampling that makes it appear discontinuous. Active testes were robust and spherical in external appearance. Internally, they were yellowish with torturously convoluted tubules with thick epithelium. Active testes weighed more than twice those inactive. In active males the sperm ducts were white, thickened, and torturously convoluted, and the tail base was much swollen. In reproductively active *C. pumilus* (Table 41) 100% testicular activity was recorded in all months but April (30%), May (50%) and August (95%). The occurrence of testicular activity in April and May indicates a secondary peak before winter quiescence. Apparently there were a few (Table 29) active males in June amongst the undissected marked population, but these might have had semen in the distal parts of the sperm ducts and inactive testes.

In *C. namaquensis* males (Tables 40, 43) 100% had reproductively active testes, except for August (25%), though 100% had semen in the distal parts of the sperm ducts, except for November when 90% had semen in the distal parts of their sperm ducts and all had active testes.

Yolked follicles were present in *C. pumilus* throughout the year (Table 42). Yolk was deposited in follicles of 2 mm diameter, proceeding to and held at 4 mm diameter if oviducal embryos were present, as in all months, but April, May and November. Yolking of follicles for the next litter was deferred until the oviducally developing litter had at least reached pholidosis. Ovulation occurred at a mean follicle ($N = 157$) size of 7,0–8,0 × 6,0–6,5 mm.

In *C. namaquensis* (Tables 37, 39, 44) yolk deposition began with follicles of 2 mm diameter. In both species non-yolked follicles were from 0,5 to 2,0 mm in diameter, and a pearly white. There were no yolked follicles in the February (50%) and November (20%) samples of female *C. namaquensis*. Yolked follicles from 2,0 to 5,0 mm diameter were found in every sample month. In *C. namaquensis* ovulation occurred at a follicle size of 13 mm or

Table 41

Monthly condition of adult male *Chamaeleo pumilus* showing fat body weights, testes weights and dimensions, and the productive state of the testes and sperm ducts. Means are in parentheses.

		Fat bodies	Testes		Testes		Sperm duct with semen
Month	N	Weight (g)	Weight (g)	Size (mm)	Active	Inactive	distally
Feb.	3	0,005–0,319 (0,122)	0,036–0,084 (0,042)	5,0–7,0 × 3,0–5,0 (6,1 × 4,3)	100%	0%	100%
Mar.	6	0,045–0,305 (0,152)	0,009–0,078 (0,033)	3,0–7,0 × 2,0–4,8 (5,4 × 3,6)	100%	0%	100%
Apr.	8	0,004–0,051 (0,028)	0,015–0,034 (0,023)	4,5–7,0 × 2,0–4,0 (5,4 × 3,0)	30%	70%	100%
May	8	0,002–0,056 (0,026)	0,018–0,046 (0,031)	4,0–6,5 × 2,5–4,0 (5,0 × 3,3)	50%	50%	100%
June	6	0,001–0,214 (0,067)	0,014–0,047 (0,032)	3,5–7,0 × 2,5–4,5 (5,1 × 3,5)	0%	100%	20%
July	5	0,001–0,065 (0,023)	0,017–0,057 (0,031)	4,0–6,0 × 3,0–4,5 (4,8 × 3,5)	0%	100%	0%
Aug.	8	0,009–0,026 (0,018)	0,012–0,045 (0,026)	3,5–6,0 × 2,5–4,5 (4,6 × 3,5)	95%	5%	0%
Sept.	5	0,004–0,024 (0,015)	0,021–0,037 (0,028)	4,0–6,0 × 2,5–4,5 (5,0 × 3,5)	100%	0%	95%
Oct.	3	0,050–0,119 (0,074)	0,030–0,064 (0,047)	5,5–6,5 × 4,0–5,0 (6,0 × 4,5)	100%	0%	100%
Nov.	5	0,002–0,122 (0,049)	0,001–0,029 (0,011)	3,0–6,5 × 2,0–4,0 (4,8 × 3,0)	100%	0%	100%
Dec.	4	0,007–0,127 (0,046)	0,015–0,029 (0,020)	4,5–6,0 × 3,0–4,0 (5,3 × 3,5)	100%	0%	100%
Jan.	4	0,004–0,017 (0,010)	0,015–0,054 (0,033)	4,0–6,8 × 2,5–4,0 (5,3 × 3,3)	100%	0%	100%

Size of adult males examined: body weight 2,8–14,8 g $\bar{x}$ = 8,7; snout-vent 53,0–93,0 mm $\bar{x}$ = 73,5; tail 55,5–107,0 mm $\bar{x}$ = 82,3.

Table 42

Monthly condition of adult female *Chamaeleo pumilus* showing fat body weights (in grams), reproductive state of ovarian and oviducal structure expressed as a percentage of the sample, and numbers of developing oviducal eggs and embryos. (Means are in parentheses: 'S-V' denotes snout-vent. Yolked follicle sizes given are diameters.)

			Oviducal				Ovarian			
			Percentage with embryos		Number of eggs or embryos		Percentage with follicles			
							yolked		not	Corpora
Month	N	Fat body weight	≥10 mm (s-v)	<10 mm	Left	Right	≥5 mm	<5 mm	yolked	lutea
Feb.	6	0,042–0,547 (0,232)	80,0	20,0	4–12 (6,8)	4–10 (6,4)	0,0	20,0	80,0	100,0
Mar.	6	0,002–0,417 (0,209)	100,0	0,0	2– 8 (5,6)	2– 7 (4,8)	0,0	20,0	80,0	100,0
Apr.	9	0,002–0,285 (0,105)	0,0	0,0	0 0	0 0	11,1	88,8	11,1	11,0
May	8	0,004–0,291 (0,131)	0,0	0,0	0 0	0 0	37,5	61,5	25,0	0,0
June	10	0,009–0,140 (0,065)	0,0	40,0	9–12 (10,5)	9 9	20,0	20,0	40,0	40,0
July	10	0,006–0,255 (0,072)	0,0	90,0	4– 9 (6,7)	3–10 (6,7)	28,6	0,0	71,5	90,0
Aug.	7	0,009–0,082 (0,041)	0,0	40,0	5– 6 (5,5)	6– 7 (6,5)	0,0	80,0	20,0	40,0
Sep.	7	0,002–0,162 (0,050)	0,0	66,8	3–10 (5,0)	3– 8 (5,2)	16,7	33,4	66,8	66,8
Oct.	7	0,001–0,381 (0,150)	42,9	14,1	4– 9 (6,8)	5–10 (7,0)	0,0	42,9	57,1	71,5
Nov.	5	0,054–0,161 (0,101)	0,0	0,0	0 0	0 0	0,0	80,0	20,0	40,0
Dec.	6	0,023–0,145 (0,074)	16,7	40,1	5– 7 (6,0)	5– 7 (6,0)	16,7	50,1	33,4	56,8
Jan.	5	0,008–0,048 (0,023)	20,0	60,0	2– 5 (4,3)	3– 6 (4,7)	0,0	20,0	80,0	100,0

Size of adult females examined: body weight 2,1–27,3 g $\bar{x} = 11{,}8$; snout-vent 51,0–102,0 mm $\bar{x} = 78{,}8$; tail 52,0–103,0 mm $\bar{x} = 78{,}0$.

Table 43

Condition by month of adult male *Chamaeleo namaquensis* showing fat body weights, testes weights and dimensions, and reproductive state of the testes and sperm ducts. Means are in parentheses.

Month	N	Fat body weight (g)	Testes		Testes		Sperm duct with semen distally
			Weight (g)	Size (mm)	Active	Inactive	
Apr.	5	0,002–0,119 (0,036)	0,051–0,282 (0,136)	5,0–11,0 × 4,0– 7,5 (8,1 × 6,0)	100%	0%	100%
June	9	0,003–0,752 (0,270)	0,015–0,259 (0,173)	4,5–11,0 × 3,0– 9,0 (7,6 × 6,1)	100%	0%	100%
Aug.	4	0,018–0,090 (0,048)	0,067–0,215 (0,165)	8,0–12,0 × 6,5– 9,0 (10,2 × 7,7)	25%	75%	100%
Nov.	6	0,014–0,542 (0,171)	0,041–0,291 (0,141)	6,0–12,5 × 4,0– 9,0 (9,2 × 6,6)	100%	0%	90%
Feb.	6	0,030–0,518 (0,215)	0,224–0,438 (0,300)	10,0–13,0 × 6,5–10,0 (11,9 × 8,0)	100%	0%	100%

Size of adult males examined: body weight 11,7–90,1 g, $\bar{x} = 48,2$; snout-vent 75,0–158,0 mm, $\bar{x} = 112,6$; tail 46,0–105,0 mm, $\bar{x} = 74,9$.

Table 44

Condition by month of adult female *Chamaeleo namaquensis* showing fat body weights (in grams), reproductive state of ovarian and oviducal structures expressed as a percentage of those sampled, and numbers of developing oviducal eggs (Means are in parentheses: 'S-V' denotes snout-vent.)

			Oviducal			Ovarian			
				Mean number of eggs		Percentage having yolked follicles diam.			
Month	N	Fat body weight	Percentage with eggs	left	right	⩾ 5 mm	< 5 mm	no yolked follicles	Corpora lutea
Apr.	9	0,013–0,654 (0,264)	33,3	6	7	33,3	100,0	0,0	33,3
June	14	0,059–2,059 (0,928)	28,6	5	5	75,0	50,0	0,0	25,0
Aug.	5	0,057–0,076 (0,064)	60,0	5	5	66,6	33,3	0,0	33,3
Nov.	11	0,027–0,261 (0,113)	0,0	0	0	60,0	40,0	20,0	0,0
Feb.	11	0,126–2,326 (0,927)	0,0	0	0	50,0	0,0	50,0	0,0

Size of adult females examined: body weight 25,2–106,5 g, $\bar{x} = 60{,}8$; snout-vent 88,0–140,0 mm, $\bar{x} = 119{,}6$; tail 61,0–95,0 mm, $\bar{x} = 78{,}3$.

greater in diameter, the eggs being held in the oviducts (see gestation, p. 131) until laying (Table 36).

When eggs were absent, *C. namaquensis* oviducts were silvery-white, thick and crumpled; the distinct crumpled portions were similar to the incubation chambers of viviparous forms (see *C. pumilus* discussion, p. 131) and are called uterine chambers by Kasturirangan (1951). Oviducal eggs (Table 39) were found in the April, June and August samples (see also gestation, p. 135). While oviducal eggs were present, follicle yolking was held at a maximum of 4 mm diameter. When the oviducal eggs were being shelled or laying imminent, development of the next clutch proceeded.

In *C. namaquensis* there was a distinct ovarian follicular and oviducal development cycle. This was also a right-left offset cycle. That is, at one period the right side had more oviducal than ovarian eggs, with the reverse situation being true of the left side. This condition shifted for the next clutches under development, with the left side having more oviducal and less ovarian eggs. *C. pumilus* had an identical right-left offset cycling of developing embryos and follicle development.

Intra-abdominal migration of ova occurred in *C. pumilus* and *C. namaquensis*, but was not common in either. While this phenomenon in other reptiles is recorded for xantusiids, iguanids, and teiids (Mayhew 1968), it is based on the number of oviducal eggs and the occurrence of full-term or regressing corpora lutea for each side. In the chamaeleons observed this method was somewhat inaccurate, as these ovarian structures were sometimes discernible for nothing apparent in either oviduct, and vice versa, which may indicate regression of ovarian structures and resorbtion of those in the oviduct to which they were related at different paces. Hard yolk sacs bearing no trace of embryos were the only oviducal structures that could not be matched to any corresponding ovarian structure.

Saurian testicular cycles resemble those of birds, and the most common saurian testicular cycle is: (1) with spermatogenesis in late summer and autumn, occurring also during winter hibernation, with spermiogenesis taking place largely in spring, but it may occur in autumn or winter. Mature sperm enter the epididymides, and copulation usually occurs in spring; or, (2) some maintain testes and sexual accessories at maximum through the summer; or, (3) those at the extremes of their (northern) range are biennial in both sexes. Very little is known of tropical forms, and most of the knowledge is based on temperate species, especially the northern varieties.

Food, weather and moisture are some mediating effects of the cycle. Photoperiod effects are hard to gauge, since reptiles expose or shield themselves to and from light in controlling their body temperatures. Licht, Hoyer & Van Oordt (1969) found male *Lacerta sicula* and *L. muralis* to be stimulated by warmth. Licht & Basu (1967) found that *Uma scoparia* testes *in vitro* can produce reproductive products at 37 C, and do not degenerate until held at 44 C. Body temperatures of 44 C are reached by this species in summer when they are maximally active reproductively and otherwise. Thus, male *Uma* can produce reproductive products at temperatures far higher than can other vertebrates, including desert birds (Riley 1937), which are capable of spermatogenesis only in the cool of night. Mayhew (1967) has shown that apparently the amount of soil moisture during winter determines the breeding of *Uma*. Where this places *C. namaquensis* in this regard is not known, for certainly it was subject to as extreme environmental temperatures as *Uma*, but maintained lower body temperatures. Perhaps of importance here are the lung diverticula (Fig. 12) which surround the gonads in both sexes.

A problem of deciding on reproductive cycles, if any, in chamaeleons (and perhaps other saurians) is the ability of the females of some species to store sperm. The loci of sperm storage is variable, being the anterior segment of the 'vagina' in the iguanids *Callisaurus*, *Crotaphytus*, *Holbrookia*, *Phrynosoma*, *Sceloporus*, *Urosaurus* and *Uta*, the tube between the oviduct and infundibulum in the gekkonids *Coleonyx* and *Phyllodactylus* (Cuellar 1965), and the distal part of the oviduct in *Chamaeleo basiliscus*, *C. chamaeleon* and *C. lateralis* (Saint Girons 1962), and in *C. pumilus* and *C. namaquensis* (this study). Such structures contain large numbers of spermatozoa in females isolated from males for several months, permitting production of one or more fertile clutches or litters. As Cuellar observes, sperm storage permits an effective lengthening of the period of fertile egg-laying.

Little value for sperm storage in *C. namaquensis* can be seen, since the males were reproductively active throughout the year, the sex ratio was almost equal, and both sexes were readily available spatially and temporally to each other. In *C. pumilus* sperm storage has a decided value, especially for the first litter in September of the reproductive year. Cape winters feature considerable rain and quite low temperatures from June to at least October, though such inclement weather may begin as early as the end of April and persist into mid-December. Males were totally inactive in July and August, thus sperm storage in *C. pumilus* females guarantees the first litter and possibly the last, independent of the availability of sexually active males at those times.

Data on viviparous chamaeleons show that *Chamaeleo pumilus* is generally credited with rarely more than one birth per year, corresponding to the Southern Hemisphere summer (FitzSimons 1943; Von Frisch 1962; Bustard 1963; Spence 1966), but only Wager (1958) agrees with this study that litters are multiple, being recorded in February to May, September, November and December. Bustard (1966) records *C. bitaeniatus* births in April, May, July and September to November, and *C. hohnelii* births in August and September (Bustard 1965). Busack & Busack (1967) record November and February births for *C. pumilus*, and Atsatt (1953) February to May, July and November. However, almost all of these records are based on captives, and Atsatt's records of November, April and May 'births' are due to injection with pituitrin of a single female *C. pumilus*. This study's records are of individuals in the field, supplemented with data on captives.

Fig. 12A–C.

The lung, air sac relationship to gonads in *Chamaeleo namaquensis* (A–B) and *C. pumilus* (C).

A. Lung (part between '8' and '11' on mm rule) at expiration shown to the top of black small intestine, and anterior to right ovary. Note large yolking follicles in both ovaries; large white stomach to right of left ovary, and juncture with small intestine and its black visceral peritoneum.

B. Lung (centre left above black small intestine) at almost full inspiration, totally obscuring ovary, which is forced dorsally and medially. (The fat bodies, very large in this female, have been partially excised to improve visibility of other structures.) Especially note transparent (clearer in Fig. 12A) abdominal peritoneum of this species. (Anterior is to left in this photo.)

C. Male *C. pumilus* (anterior to right) with lung at almost full inspiration, almost obscuring right testis, which is abnormally lacking a black visceral peritoneum and appears white. Its opposite number, just posterior to (normal position of gonads), and below it in photo, has usual black visceral peritoneum. Note everted hemipenes, fat bodies just anterior to pelvis, and black visceral and abdominal peritoneum. Air sacs (a partly-filled air sac is marked by black arrow in Fig. 12B) are attached to posterior part of lungs only in *C. namaquensis*. Scale in mm.

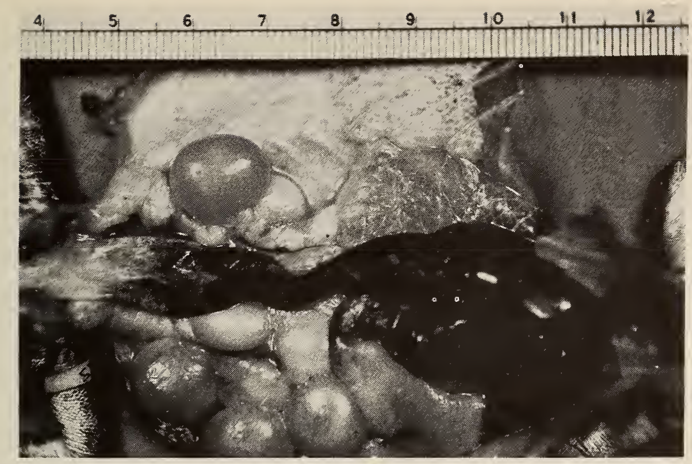


Fig. 12A.

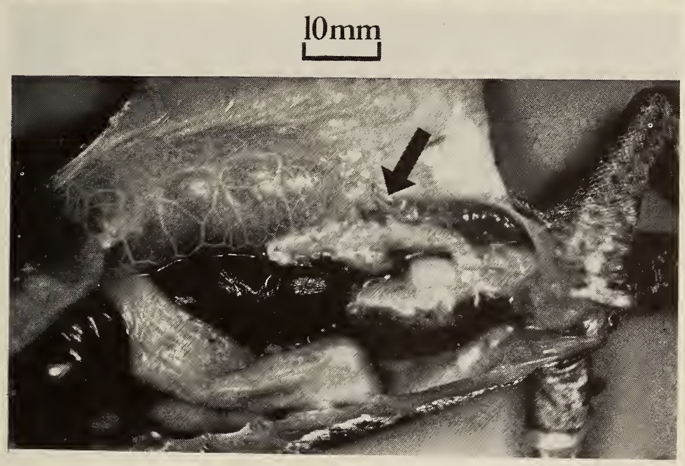


Fig. 12B.

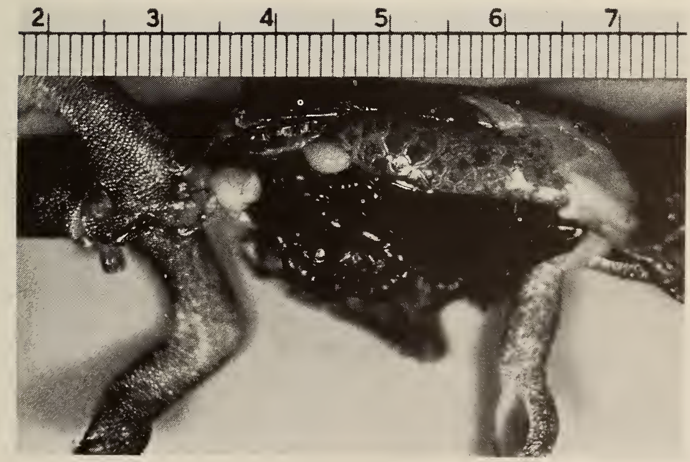


Fig. 12C.

Discussion and review of the complex reptilian reproductive cycles are given by Parkes (1956), Miller (1959), Forbes (1961) and Mayhew (1968), almost all of which deal with north temperate reptiles and virtually no complete information is given on chamaeleons. Bons & Bons (1960) found the Mediterranean *Chamaeleo chamaeleon* mates in August or September and lays eggs in October and November, which is the tropic cycle with egg-laying during or at the end of the rainy season, and not of the Mediterranean, with egg-laying at the end of spring. Bourgat (1968*b*) found *C. pardalis* of Réunion does not have spermatogenesis during July and August (winter). The East African *C. dilepis* lays its eggs in March (Wager 1958), September, just after the rainy season (Milner 1949), late summer (FitzSimons 1943), February (Cott 1934) and February to April (Brain 1961). Of West African chamaeleons, *C. gracilis* lays its eggs in September at the end of the rainy season (Menzies 1958), while *C. basiliscus* lays its eggs in December in captivity (Shaw 1960). *C. chamaeleon zeylanicus* of India lays its eggs in November (Trench 1912).

Ovarian cycles of reptiles are of several types, which are not yet possible to correlate to taxonomic, geographic, or climatic differences: (1) much yolk is deposited shortly prior to ovulation, but subsequent to a long slow initial growth of the ova; (2) yolk deposition occurs gradually through most of the year preceding ovulation; (3) yolk deposition occurs shortly after ovulation and mature ova occur in the ovary through the winter; (4) two sets of ova are produced and ovulated per year, each set being formed directly after ovulation of its predecessor; (5) non-seasonal breeders, producing at any time of the year. The mediating effects of the male cycle have been alluded to and presumably also act on the female cycle. For example, Tinkle & Irwin (1965) found *Uta* females to be stimulated by warmth, as did Marion (1970) for female *Sceloporus undulatus*.

10. *Gestation*

The corpora lutea of *Chamaeleo pumilus* appear as yellowish-white, imperfect doughnut-shaped structures as large as 4 × 2 mm in females that have recently ovulated, maintaining a diameter of 2 mm throughout pregnancy. Corpora lutea of the previous litter were distinct at 1,8 mm diameter, but whitish, for some time during the term of the next successive litter. Gestation in *C. pumilus* was as short as 60 days in the case of litters conceived in March and born in May, when subjected to the hottest environmental temperatures, but at other times gestation was as long as approximately 90 days. The overall ($N = 56$), average gestation period was 72 days. Those conceived in April and May and born in September did not begin oviducal development until mid-June, or the latter part of July. Three months is the approximate gestatory period for all reported viviparous chamaeleons, *C. pumilus* (Atsatt 1953; Wager 1958; Von Frisch 1962; Bustard 1963; Spence 1966; Busack & Busack 1967), *C. bitaeniatus* (Bustard 1966) and *C. hohnelii* (Bustard 1965). This study cannot agree with Rose's (1950) casual observation that gestation in *C. pumilus* is, '. . . well over a year'.

Pregnant *C. pumilus* nearly always maintained a Colour Index of '5', and, as such, were most conspicuous in their habitat and by their habits, being abroad in inclement weather, long after the males and non-pregnant females had sought shelter in the depths of the bushes. This greater activity of pregnant females made them seem the predominant sex. Bourgat (1968*a*) notes that gravid *C. pardalis* are the most active individuals. Continually basking pregnant females improve development of their winter-borne young. The dermal melanin deposit, the black abdominal, and uterine visceral peritoneum protect the young from the intense insolation they were subjected to. Pregnant females in warm months basked far less frequently, sought shade, and were lighter. Young were quite harmed by excessive heat. In laboratory tests 5 pregnant females that were subjected to temperatures above 35 C gave birth, usually prematurely, to 56 young, of which 20% had malformations of the eyes and/or head, 1% were club-tailed, and 10% were still-born.

Developing oviducal eggs (*Chamaeleo namaquensis*) and embryos (*C. pumilus*) are arranged longitudinally in the oviducts on either side of the mid-line. As they develop, the eggs (*C. namaquensis*) and embryos (*C. pumilus*) take up more and more space until they almost fill the posterior part of the coelom, but unlike many other lizards the viscera are not crowded anterior of their normal position, rather they are forced ventrally. The developing oviducal eggs (*C. namaquensis*) and embryos (*C. pumilus*) are offset, so that the egg or embryo in the contralateral oviduct more or less fits between two eggs or embryos in the ipsilateral oviduct, with the viscera forced ventrally. Such an arrangement allows both species to continue their voracious feeding in maintenance of their high metabolic rates. *C. pumilus* fed until a few days prior to birth; *C. namaquensis* never stopped.

In *C. namaquensis* the corpora lutea are about 2 mm in diameter and held at that for the entire gestatory period of 35–45 days. They regress rapidly after oviposition, though some were recognizable at the time of ovulation of the next successive clutch. In those five *C. pumilus* that had corpora lutea excised, there was no effect on litter development of foetuses that had passed pholidosis. But in those with less mature embryos, these young were resorbed. In the four gravid *C. namaquensis* excision of corpora lutea did not affect those eggs near oviposition, but resorbtion resulted of eggs recently ovulated. *C. namaquensis* eggs are ovulated at sizes of 13 mm or greater in diameter, and are very large at oviposition showing a clearly marked embryonic development. Compared to the eggs of other oviparous chamaeleons so far examined, the highly advanced states of development of recently oviposited eggs of *C. namaquensis* may indicate that this species is developing ovoviviparity.

The oviducts of *Chamaeleo pumilus* have distinct incubatory chambers (Figs 13, 14), each of which is supplied from a single large artery and drained by a prominent vein running dorsally along the surface of the oviduct in mid-line. These chambers are similar to those described by Weekes (1935) and Kasturirangan (1951). *C. pumilus* oviducts maintain their shape even between

Fig. 13.

A. Excised oviduct of *Chamaeleo pumilus* showing 10 full-term foetuses near birth, their yolk supplies exhausted, and one egg being resorbed, which has been excised from the oviduct and is in centre of photo. In excised ovaries (just to left of egg being resorbed) note 10 corpora lutea for full-term foetuses in upper ovary, which matches this oviduct. The egg being resorbed has long since lost its corporus luteum.

B. Incubatory chambers of an excised *C. pumilus* oviduct (anterior at top of photo). Incubatory chamber at top has had an egg (embryo and yolk sac at top) removed to show vascular supply of chamber. Egg at bottom of photo has had egg membrane peeled off, which is shown immediately to the right to show foetal vascular supply. Note, at extreme right of photo, egg not in a defined incubatory chamber, undergoing resorbtion. Scale in mm.

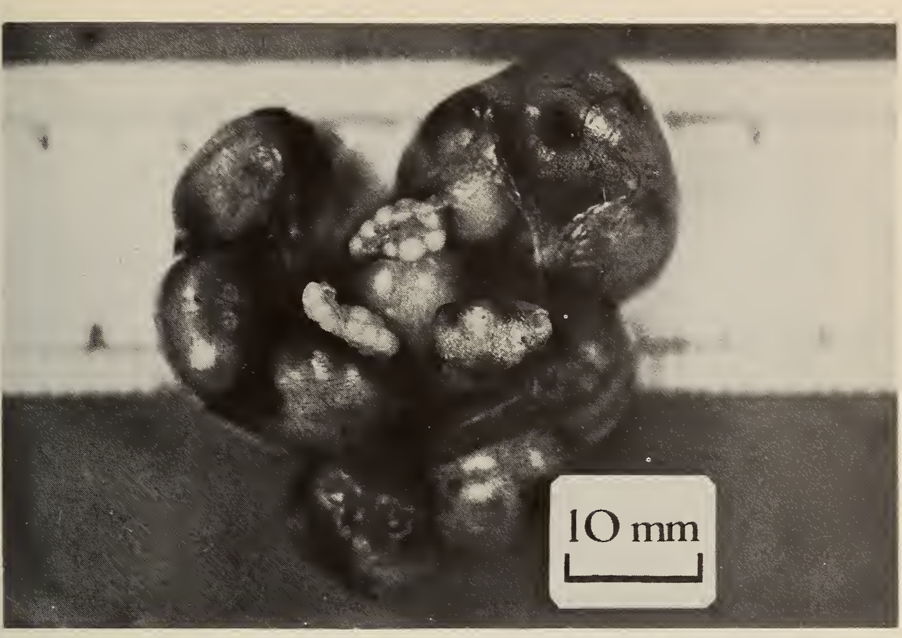
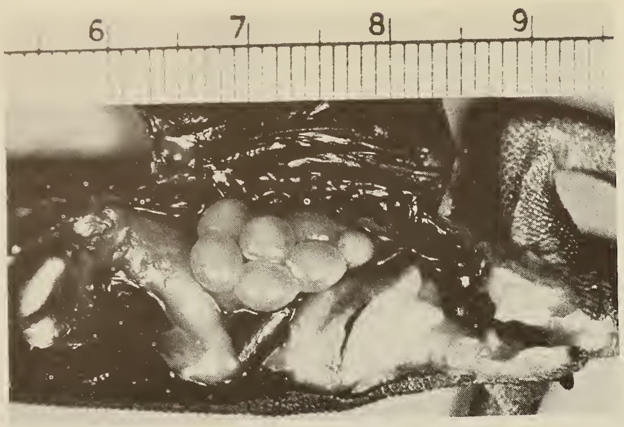
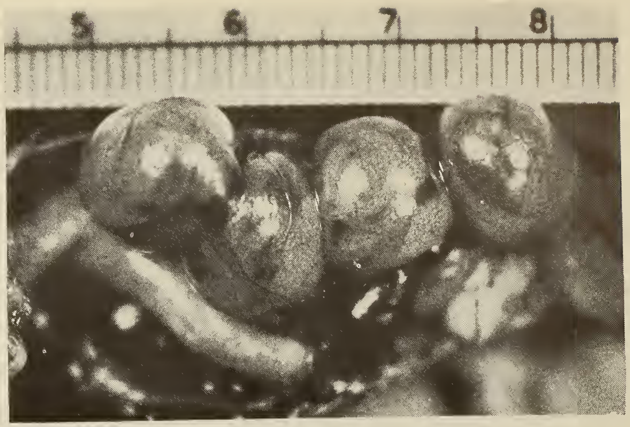


Fig. 13A.

Fig. 13B.



A



B

C

Fig. 14.

A. Female *Chamaeleo pumilus* (anterior to left in this photo) dissected to show large ovarian follicles nearing ovulation. Note large fat bodies at bottom right of abdominal cavity; black abdominal and visceral peritoneum of small and large intestines; large white stomach, part of which is shown going obliquely from top left of, to centre of body cavity, just anterior to left ovary (right ovary obscured).

B. About three weeks from birth, large, full-term foetuses in their incubatory chambers of left oviduct of a *C. pumilus*. Note white stomach passing obliquely just anterior of and below oviduct, also somewhat indistinct (but smaller than in Fig. 14A) whitish fat bodies in bottom right.

C. Excised oviducts of *C. pumilus*, showing right to left: newly ovulated eggs; full-term foetuses, with pholidosis complete and undergoing pigmentation (most of their yolk is depleted); younger foetuses, just starting pholidosis, with their yolk supplies still noticeable. Oviducts excised from different females. Scale in mm.

pregnancies and the chambers are distinct, crumpled areas. The placentae of *C. pumilus* are best assigned to Weekes' Type 'I', since the yolk content of the eggs is not markedly reduced at ovulation. Recently ovulated eggs (7,0–8,0 × 6,0–6,5 mm) often have a developing embryonic area of 2–4 mm diameter. In *C. pumilus* the yolk sac placentae eventually gives way to an allanto-placentae, and most young about two weeks from birth have empty yolk sacs. Good reviews of viviparous adaptations in other reptiles and the maternal-foetal relationship are those of Boyd (1942), Cate-Hoedemaker (1933), Flynn (1923), Hoffman (1970), Wislocki (1920) and Mossman (1937). Reptiles show all gradations from the simplest maternal-foetal relationship to conditions little removed from that in eutherian mammals.

The occurrence of two closely spaced births, or two markedly different foetal age groups within the same oviducts of *C. hohnelii* (Parker 1940), *C. pumilus* (Atsatt 1953; Busack & Busack 1967) and *C. bitaeniatus* (Bustard 1966) has been attributed to secondary fertilization via sperm storage, or superfoetation, that is, two pregnancies from one mating. In these observations two closely-spaced births occurred in the September litters. Bustard (1966) thinks none of the suggested interpretations is wholly valid, as some of Parker's material is explained as atretic eggs which are being resorbed. Parker thought that such occurrences indicated all is not well. Ectopic embryos were observed in *C. pumilus*, one of which was a 'lithopedion', well-advanced and with partial adult type coloration. It was affixed to the fat body.

Since pregnant female chamaeleons resist mating, any subsequent fertilisation would be most likely from sperm storage. *C. pumilus* eggs being resorbed were all ones that were not in incubation chambers, nor were full-term corpora lutea present for them, only atretic corpora lutea at best. This indicates that on some occasions, viviparous chamaeleons ovulate more eggs than there are gestation sites for. Such eggs would face resorbtion, and the data showed this to be so. In September, *C. pumilus* had two litters of very small size (no more than 8 young in each) that were probably conceived via sperm storage by direct mating in April and May. They were probably small, because they developed over winter in the female, on whom they must have been a considerable drain during this inclement season. Both were ovulated in mid-June or the latter part of July, apart from each other, the second litter being potential and held in the ovary at a follicular size of greater than 5 mm diameter. However, triggered by oviducal site availability, the female's physiological state, and/or other conditions favouring the development of a larger first of the year litter size, a second small September litter proceeded (ovulated) to oviducal development. The relationship of the difference of follicle sizes and developing embryos is shown in Tables 37 and 42. The September litters had the least variation in complement of any litter. The time of parturition between these two differently conceived litters was no more than two days in marked females in the field. Some captives did stretch parturition over a week, perhaps reflecting nutrition problems of captivity. The second September litter is best considered as superfoetation, conceived at and beginning oviducal development at a closely spaced but later time from the first September litter. Both September litters were essentially born at the same time and have been treated as single litters (Table 38). The single small litters born in May were conceived by direct mating in February and March and represented a means of achieving a litter at the warmest time of the year. This allowed for recovery of the reserves of the female before development of the September litter.

Chamaeleo namaquensis eggs grew from the ovulatory size of 13 mm or greater in diameter to a mean of 20,5 × 11,6 mm; 1,5 g (max 26,0 × 14,5 mm; 2,8 g) in 25–30 days (warm season), 35–45 days (cool season) at the time they were oviposited. A small, reddish embryonic area 2 mm diameter was visible in a few recently ovulated eggs, and at the time of oviposition this area was as great as 10 mm. The oviducts of *C. namaquensis* contained distinct 'gestatory' chambers, each of which housed an egg. The vascular supply to such chambers was, however, less distinct than that of the incubatory chambers of the viviparous forms.

Brain (1961) gives a 120-day gestation period for *C. dilepis*. The gestation period of *C. namaquensis* is closest to *C. chamaeleon zeylanicus* (Trench 1912) and *C. chamaeleon* (Bons & Bons 1960) of reported oviparous chamaeleons, and to some iguanids (Burrage 1966).

11. *Incubation*

The overall incubation increment of *C. namaquensis* eggs was: length: 14–40% ($\bar{x} = 19{,}8\%$); width: 4–16% ($\bar{x} = 9{,}8\%$); weight: 18–65% ($\bar{x} = 37\%$). In just two days of incubation, length increased by 4–19% ($\bar{x} = 8{,}2\%$); width 4–9% ($\bar{x} = 6{,}0\%$); weight 12–40% ($\bar{x} = 27{,}3\%$). Increments after 60 incubatory days were slight and essentially as for the entire period. During the later stages of incubation, the large, black developing *C. namaquensis* embryo was clearly discerned through the shell. Increments for the first two and 60 incubation days were less in those clutches laid in May through July, which had the longest incubation period (May, 112; June, 100; July, 97 days). Eggs laid in early August took 91 days, as did those laid in October and September, and those of late August took 92 days. The overall (N = 250) incubation time was 98,4 days.

The following data are available in the literature on incubation times of chamaeleon eggs: *Chamaeleo dilepis:* 90 days (FitzSimons 1943), 219–365 days (Milner 1949; Wager 1958; Brain 1961); *C. gracilis:* 210 days (Menzies 1958); *C. basiliscus:* 179 days (Shaw 1960); *C. chamaeleon:* 280 days (Haas 1947), and 250–260 days (Bons & Bons 1960). It was accounted by people at Cape Cross South West Africa, that *C. namaquensis* eggs laid there took twelve months to hatch. However, this is thought to have been multiple usage by several females of the same nest site, with different hatching times of the several clutches laid at various dates. Or, conversely, different clutches laid at different dates by one, perhaps two females. On the average, chamaeleon eggs take longer to hatch than those of other saurians, but about the same time as the Australian deserticulous agamid *Moloch horridus* (56 days, White 1948; 90–132 days, Sporn 1965). Many of these chamaeleon incubation times are based on captive records, under different conditions, clutches at different times of the year, and for clutches laid by females of widely separated geographic populations.

The effect of temperature on incubating saurian eggs has been discussed in several papers, with the expected observation that longer incubation obtains at cooler times of the year. Cooper (1965) experimentally incubated clutches of lacertid eggs at different temperatures, finding maximum incubation time (122–160 days) accrued when the eggs were subject to temperature variation (18,5–21,0 C by day; 12,5 C by night), and least (46 days) when the eggs were incubated at a uniform 27 C. Great disparity has been recorded in the incubation time of the eggs in natural nests of the American scincid *Eumeces fasciatus*, Fitch (1954) giving 27–47 days, and Cagle (1940) nine days. Undoubtedly, as Fitch (1954) asserts, temperature is important, but it may not be the only factor. Burrage (1966) discusses the influence of different thermal gradients of various substrates on incubation times of the eggs of *Uta*, noting that site selection at oviposition is also important, since some substrates are more favourable throughout the year. Bons & Bons (1960) have shown that chamaeleon eggs do not hatch quicker when maintained at higher temperatures (27–28 C), but gross cephalic deformities result. Table 45 shows the temperatures of dune sand and gravel for inland and coastal sites at the 200–250 mm depth where *Chamaeleo namaquensis* laid its eggs. There was some difference in sand and gravel temperatures, but markedly higher inland substrate temperatures occurred especially in June and July, when fog was the rule at coastal sites. The greater prevalence of fog and the moderating effect of the Benguela Current depressed coastal air and surface substrate temperatures. The surface substrate maximum temperature, occurring at approximately 14:00 hours, was only reflected the following day at a depth of 200–250 mm. No oviducal eggs were found November to March (Tables 39, 44), which might be because the temperature at the

Table 45

Twenty-four hour substrate temperature (in °C) records at 200–250 mm depth for dune sand and gravel at coastal and inland locations. Means are in parentheses.

	Coastal		Inland	
Month	Dune sand	Gravel	Dune sand	Gravel
1969				
April	23,5–28,5	23,0–28,0	27,0–35,5	25,0–31,0
	(26,5)	(25,5)	(31,5)	(28,5)
June	15,0–20,0	14,0–21,0	21,0–30,0	20,0–33,5
	(17,5)	(17,3)	(26,0)	(24,5)
November	22,0–31,0	21,0–33,0	26,0–33,0	27,5–34,0
	(25,5)	(25,0)	(29,5)	(31,0)
1970				
February	27,0–35,0	25,0–33,0	32,0–39,0	31,0–39,0
	(30,3)	(28,6)	(35,5)	(34,0)

laying depth was too high from February to April. At this time all the young had hatched and in the May clutch development proceeded only in late April as cooler temperatures returned at the laying depth. Regardless, *C. namaquensis* eggs incubated at temperatures above the 27–28 C 'harm' limit of Bons & Bons (1960), indicative of adjustment to their environment.

12. *Young*

Birth size data for *Chamaeleo pumilus* are given in Tables 38 and 47. The young for most litters averaged a snout-vent length of about 22 mm—the tail usually equal to or slightly less than this, and rarely in excess, regardless of sex—and a weight of 0,3–0,4 g. The smallest young (snout-vent $\bar{x} = 20$ mm) were those born in September, perhaps reflecting the effects of superfoetation, and the largest young (max snout-vent 27 mm; $\bar{x} = 25$ mm) were born in November. Males were slightly smaller than females. Table 46 gives the sex and pattern types of newborn *C. pumilus*. Recently born viviparous chamaeleons resemble the adults, except in colour and pattern, though some (Table 46), mostly males, had a true adult pattern. Brown individuals at birth were mostly females, and did not acquire the adult colour at maturity. The disparity in pattern between the young and adult of viviparous chamaeleons is noted for *C. pumilus* by Abel (1931), Von Frisch (1962) and Bustard (1963); *C. bitaeniatus* (Bustard 1966); and *C. hohnelii* (Angel 1933; Bustard 1965). The sex ratio at birth in *C. pumilus* was nearly equal. Von Frisch (1962) thinks that the newly born young of *C. pumilus* have to 'learn' to aim their tongues, but Bustard (1966) does not agree, with which this study concurs. However, it was observed that slightly premature young aimed poorly at first, but improvement of their aim is probably due to maturation of their senses, rather than 'learning'.

Table 46

Sex and pattern types at birth of 614 *Chamaeleo pumilus* expressed as percentages. The number not enclosed in parentheses shows the percentage of a given sex having a particular pattern type, while the number enclosed in parentheses shows the percentage of that sex of that particular pattern type in the total sample.

		Pattern types							
Sexes		Adult		Gray-green		Gray		Brown	
Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
38–64	36–62	50,0	16,5	25,0	26,4	15,0	23,1	10,0	34,0
$\bar{x} = 51$	$\bar{x} = 49$	(20,0)	(10,0)	(10,0)	(16,0)	(6,0)	(14,0)	(4,0)	(20,0)

Data on *Chamaeleo namaquensis* oviposition and hatching dates and the time to reach maturity are given in Table 49. Recently hatched male *C. namaquensis* varied in total length from 45,0–55,0 mm (20,0–25,0+25,0–30,0 mm); means: total length: 50,0 mm; snout-vent: 22,5 mm; tail: 27,5 mm; and all weighed about 0,6 g. Females were larger, varying in total length from 55,0–65,0 mm (30,0–35,0+25,0–30,0 mm); means: total length: 60,0 mm; snout-vent: 32,5 mm; tail: 27,5 mm; and weighed 1,0–1,7 g ($\bar{x} = 1,5$ g). The young were mere miniatures of the adults as to pattern and colour, but possessed more vertebral knobs (see also FitzSimons 1943). *C. dilepis* (Brain 1961) and *C. basiliscus* (Shaw 1960) hatchlings are also miniatures of their adults. *C. namaquensis* young hatched out late in the evening and during the night, and rapidly dispersed. Unlike the adults, they preferred to climb and could be found on grass stems and other vegetation, or perched on rocks. (A February hatchling, photographed in early March, is shown in Figure 11.)

13. *Growth and longevity*

The growth of young *Chamaeleo pumilus* is shown in Table 47. As time passed, the size differences narrowed between the various litters. Data on juvenile *C. pumilus* fat body weights, gonadal sizes and weights are given in Table 48. In *C. pumilus* and *C. namaquensis* juvenile testes were flattish with thin, whitish epithelium, and loosely convoluted tubules; the sperm ducts were flat and thin, whitish opaque, straight to wavy. In females the oviducts were collapsed and thin, black in *C. pumilus*, and silvery in *C. namaquensis*. The ovaries were longer than they were wide and somewhat transparent, bearing follicles no larger than 1,5 mm diameter. Upon hatching and at birth, follicle size was not more than 0,25 mm, and the entire ovaries were about 2,0 × 1,0 mm. The testes were about 1,0 × 0,75 mm and translucent.

Table 47

Mean growth rates to maturity of 148 *Chamaeleo pumilus* in the field. Both sexes mature at a snout-vent length of 50 mm. Roman numerals represent months.

Birth date	Mean snout-vent (mm) at birth	Mature date (days)
II	22,0	210
III	22,0	240
IV	22,0	240
V	22,0	240
IX	20,0	169
XI	25,0	85
XII	22,0	108

Busack & Busack (1967) give data on the growth of a November brood of 12 *Microsaura pumila* (= *C. pumilus*) over 300 days, some of which present different growth curves. One of Busack & Busack's young chamaeleons reached 60 mm (snout-vent) in 175 days, another measured 37 mm (s–v), and one 43 mm (s–v) in 135 days. One chamaeleon reached 60 mm (s–v) in 262 days, and another did not grow in 143 days from 20 mm (s–v) at birth. Half of Busack & Busack's sample did not live over 50 days. Bustard (1965) records a male *Chamaeleo hohnelii* that increased in 18 days from a total length of 95 to 110 mm, acquiring sexual maturity, though he is not sure of its exact age.

Table 48

Juvenile male and female *Chamaeleo pumilus* and *C. namaquensis* showing fat body weights, testes weights and dimensions, weights and dimensions of ovaries and ovarian follicle size. Sizes are in millimetres; weights in grams. Means are in parentheses.

		Testes	
Males	Fat body weight	Weight	Size
C. pumilus	0,001–0,015 (0,006)	0,003–0,010 (0,006)	1,0–3,5 × 0,8–2,0 (2,1 × 1,3)
C. namaquensis	0,001–0,003 (0,002)	0,002–0,003 (0,002)	2,5–3,0 × 1,5–2,0 (2,7 × 1,8)

Size of 24 juvenile *C. pumilus* examined: body weight 0,3–1,4 g $\bar{x}$ = 0,8; snout-vent 27,5–46,0 mm $\bar{x}$ = 34,9; tail 25,0–44,0 mm $\bar{x}$ = 34,7.
Size of 7 juvenile *C. namaquensis* examined: body weight 3,0–7,0 g $\bar{x}$ = 4,0; snout-vent 40,0–46,0 mm $\bar{x}$ = 42,0; tail 30,0–37,0 mm $\bar{x}$ = 33,5.

		Ovary		
Females	Fat body weight	Weight	Size	Follicle size
C. pumilus	0,001–0,080 (0,040)	0,002–0,010 (0,006)	1,0–4,0 × 0,5–3,0 (2,5 × 1,5)	0,5–1,5 (0,7)
C. namaquensis	0,001–0,091 (0,071)	0,003–0,013 (0,008)	1,3–4,1 × 0,7–3,2 (3,4 × 1,9)	0,5–1,5 (0,7)

Size of 32 juvenile *C. pumilus* examined: body weight 0,4–2,5 g $\bar{x}$ = 1,0; snout-vent 24,0–51,0 mm $\bar{x}$ = 31,2; tail 23,0–51,0 mm $\bar{x}$ = 31,5.
Size of 6 juvenile *C. namaquensis* examined: body weight 3,0–4,0 g $\bar{x}$ = 3,8; snout-vent 30,0–37,0 mm $\bar{x}$ = 33,0; tail 29,0–33,0 mm $\bar{x}$ = 32,0.

C. pumilus and *C. namaquensis* in the field grew faster and less erratically than those in captivity. A captive *C. pumilus* grew faster than those viviparous chamaeleons reported in the literature, but some registered the same sort of erratic growth and there were runts, who grew little or not at all. Also, most literature references do not record the sex of the young.

Table 49 shows growth rates for *C. namaquensis* young from hatching to maturity. Females reached maturity in 150 days at a snout-vent length of 75–80 mm. Males reached maturity in 210 days at a snout-vent length of 70–75 mm. Table 48 shows fat body weights, gonadal sizes and weights of juvenile *C. pumilus* and *C. namaquensis*. Growth was steadier and faster in female *C. namaquensis*; while the overall male growth rate was slower it was faster over the first and last 30 day periods (3 mm per diem). Juvenile *C. namaquensis* preferred climbing and were far more adept at this than adults. Their thermoregulatory pattern was adult in every respect. As they neared maturity, their increased stockiness and larger size made for injurious falls, when they tried climbing the same structures that easily supported them at a smaller size.

Table 49

Mean growth rates to maturity of 107+ *Chamaeleo namaquensis*, mostly in the field. Males matured in 210 days at a snout-vent length of 70–75 mm; females matured in 150 days at a snout-vent length of 75–80 mm.

Month eggs laid	Incubation period (in days)	Sex	Number of days for young to reach maturity
May–July	97–112	♂♂	210
		♀♀	150
August	91	♂♂	210
		♀♀	150
August–September	91– 92	♂♂	210
		♀♀	150
October	91	♂♂	210
		♀♀	150

Considerable differences have been reported for the growth of oviparous chamaeleons. Brain (1961) feels that *C. dilepis* takes a long time to acquire maturity, citing a two-year-old that was still juvenile and sexually immature. However, Wager (1958) notes a *C. dilepis*, 45 mm long at hatching, had reached 152 mm seven months later. After seven months the growth of this individual slowed, and at 13 months its total length was 216 mm, having gained only 63 mm in the final six months of observation. Wager thinks *C. dilepis* matures in a year. The growth rate of chamaeleons does not seem unusually slow or fast in comparison with that of other saurians recorded in the literature (Mayhew 1968) and the influence of hatching times of different clutches of different species and populations undoubtedly varies, as the geographic and climatic conditions obtaining in the respective areas each inhabits. Menzies (1958) reports that *C. gracilis* hatch at the onset of the rainy season, which might be inclement enough to retard growth. *C. namaquensis* was little affected by rainy seasons, and all young hatched out after the fogs of June and July. Furthermore, food in the Namib Desert was always abundant and young and old chamaeleons gorged to the limit; a condition not often enjoyed by captives, whose feeding by their captors is an exhausting task (see also Abel 1931 and Bustard 1963). As Bustard (1963) observes, captive chamaeleons are at a liability, the limits of captivity showing the mere minimum they are capable of.

There is no good knowledge of the life-span of chamaeleons, though Brain (1961) feels that *C. dilepis* reaches 10–20 years, and hearsay puts *C. pumilus* at a maximum of six years. Three years of study on marked *C. pumilus*, showed amazing longevity of individuals in the field, some 40% of the adults, plus some progeny recorded and marked in February, 1969, being recovered in February, 1971. *C. namaquensis* was not observed over a long enough period—though recovery was quite high—but, as with *C. pumilus*, and as Bourgat (1968*a*) observed for *C. pardalis*, there was tremendous fluctuation according to the season. At the end of a year he recovered 60 of 140 he had marked.

IV. Summary.

Various aspects of the life histories of the chamaeleonids *Chamaeleo pumilus* (Gmelin) and *C. namaquensis* A. Smith were investigated in the field and laboratory from 13 January 1969 to 30 November 1970 in the Republic of South Africa and South West Africa. A total of 494 *C. pumilus* and 207 *C. namaquensis* were marked for field studies by branding or leg bands. *C. pumilus* inhabit any vegetation guaranteeing a plentiful source of prey. They were studied at Port Nolloth, Leeu-Gamka, Beaufort West, Van der Stel station, The Strand and chiefly at Stellenbosch. While primarily of arboreal habits, *C. pumilus* frequently walks along the ground, such ground-dwelling habits being especially true of those inhabiting arid and semi-arid areas. *C. namaquensis* is ubiquitous in desert and near desert areas. Adults are exclusively ground-dwelling, even invading the desert littoral intertidal zones. *C. namaquensis* was observed in South West Africa at Gobabeb, Tsondab, Geluk Farm, Solitaire, Rehoboth, and on the coast from Walvis Bay north to Cape Cross.

The only recorded instance of ectoparasites were *Culex* mosquitoes feeding on *C. namaquensis* at Gobabeb. There was some seasonal and sexual variation in the incidence and degree of endoparasitism in *C. pumilus*, the females harbouring more parasites than the males. The nematode *Strongyluris* was the principal intestinal helminth of *C. pumilus*. The cestode *Oochoristica africana* was the principal intestinal helminth of *C. namaquensis*. Cysts and larval worms occurred in both chamaeleons. Snakes and birds were the principal predators on *C. pumilus*. Raptorial birds were the chief predators on *C. namaquensis*. Physical factors and human activities also affect chamaeleons.

The body temperatures of 549 *C. pumilus* active in the field ranged from 3,5 C to 37,0 C (mean 22,4 C; median 22,8 C). The body temperatures of

351 *C. namaquensis* active in the field ranged from 14,0 C to 39,7 C (mean 28,7 C; median 28,8 C). In laboratory preferred body temperature gradients, 20 *C. pumilus* were active from 7,0 C to 30,0 C (mean 25,0 C) and 18 *C. namaquensis* were active from 18,5 C to 36,2 C (mean 29,3 C). While body temperatures of *C. pumilus* varied according to the weather and season, those of *C. namaquensis* were much more stable, though the body temperatures of inland and coastal populations differed slightly. Field records of nocturnal body temperatures of both species at rest were close to the environmental temperature, while those in captivity were slightly higher.

Chamaeleons regulate their body temperatures by a complexly integrated physiological process, involving dermal colour lability with attendant vasomotor and other cardiovascular adjustments, body posturing, thermo-pneumatic changes in the volumes of the lungs and air sacs, and panting. The role of dermal colour lability was examined in laboratory experiments using 30 *Chamaeleo pumilus* and 28 *C. namaquensis*. Dark-adapted chamaeleons are warming, light-adapted individuals are cooling. By changing the body contour by compression and posturing, chamaeleons regulate the heat and light load striking their bodies. At any given temperature, the heart rates of 5 each of *C. pumilus* and *C. namaquensis* were higher during heating than cooling. Live chamaeleons heated faster than they cooled, whereas dead ones heated and cooled at the same rate.

The peak oxygen consumption in 15 *C. pumilus* was at 25 C, while the greatest active Q_{10} (1,29) value was over the 5–15 C range. The peak oxygen consumption of 15 *C. namaquensis* was at 35 C, while the greatest active Q_{10} (2,91) value was over the 25–35 C range.

C. pumilus and *C. namaquensis* were active throughout the season under all weather conditions, and were active from about sunrise to sunset, except ovipositing *C. namaquensis* were active throughout the night. Many newly hatched *C. namaquensis* came out during the night.

Partially blinded chamaeleons either naturally or experimentally developed an accuracy of 57,0–63,0% ($\bar{x} = 60{,}0\%$) in catching prey, whereas the accuracy of normal *C. pumilus* was 75,0–92,0% ($\bar{x} = 86{,}0\%$) and that of *C. namaquensis* was 80,0–90,0% ($\bar{x} = 85{,}0\%$).

In *C. pumilus* the tongue can pull a weight equal to two-thirds or one-half of the body weight and be maximally projected to a length about two-thirds of the total length of the animal. In *C. namaquensis* the tongue can pull a weight equal to the body weight of the individual chamaeleon and be maximally projected to a length equivalent to that of the snout-vent of the animal. The prey is held by a mechanical overlapping of the bi-lobed tongue knob at the tip of the tongue.

By selecting prey of certain sizes, both chamaeleons could realize a greater intake of food than by eating very large prey items. *C. pumilus* realized maximal ingested volumes by selecting muscid flies, its principal prey, and small tenebrionid beetles. *C. namaquensis* realized its greatest daily volumes of food when meals were composed of small locustids and large tenebrionids. *C. namaquensis* took about 19 or 23 large tenebrionids per meal, with a minimum of 5 to a maximum of 15 (x̄ = 12) daily meals. *C. pumilus* and *C. namaquensis* were voracious feeders and rapidly food. Two to five hours were required to digest and eliminate meals taken in during the day and up to 12 hours for meals taken before retirement and digested overnight.

In *Chamaeleo pumilus* (♂♂64; ♀♀86) there were seasonal and apparently sexual variations in diet. Dipterans were the main prey item, but the families selected varied with the sex of the chamaeleons. At some times of the year the prey eaten by the females, for example, was either not the same as that eaten by the males, or the proportions taken varied tremendously. Inland (N = 64) and coastal (N = 157) *C. namaquensis* preyed mostly on large tenebrionids. Plant and inorganic matter were also ingested. Mammal hair and bird feathers occurred in inland samples, and reptiles were taken by coastal *C. namaquensis*. Strand-dwelling *C. namaquensis* fed on flies, intertidal arthropods, tenebrionids, and reptiles.

Water is of crucial importance to chamaeleons, and they cannot survive on food alone. Desiccation experiments were run on 18 each of *C. pumilus* and *C. namaquensis*. In one test they were given food but no water for 12 days and then food and water for 3 additional days. In a second test they were without food and water for 7 days. In both experimental sets, the haematocrit values of dehydrated *C. pumilus* were 28,6–33,7 (x̄ = 31,3) and plasma osmolality values 395,0–440,0 mOsm (x̄ = 421,3), and the haematocrit values of dehydrated *C. namaquensis* were 14,6–19,8 (x̄ = 17,6) and the plasma osmolality values 230,0–255,0 mOsm (x̄ = 246,3). In rehydrated *C. pumilus* the haematocrit values were 14,5–29,0 (x̄ = 21,4) and the plasma osmolality values 200,0–210,0 mOsm (x̄ = 203,8), and the haematocrit values of rehydrated *C. namaquensis* were 15,5–32,5 (x̄ = 24,6) and the plasma osmolality values 219,0–292,0 mOsm (x̄ = 261,3). These data suggest water storage in the vascular space of both chamaeleons. Seven freshly caught *C. pumilus* had haematocrit values of 29,0–30,5 (x̄ = 29,9) and plasma osmolality values of 200,0–210,0 mOsm (x̄ = 203,8). Eight freshly caught *C. namaquensis* had haematocrit values of 42,0–50,0 (x̄ = 46,6) and plasma osmolality values of 220,0–290,0 mOsm (x̄ = 259,8).

C. namaquensis has a salt gland and samples of the exudate of this showed excretion of sodium, chloride, and potassium in the ratio of 6,4: 7,0: 1,0; respectively. While this gland undoubtedly is of value in strand-dwelling chamaeleons to excrete any salt ingested with the intertidal prey on which they feed, its chief function is probably to enable *C. namaquensis* to produce a urine of low water content by re-excreting electrolytes which have been reabsorbed in the cloaca. This would greatly benefit the water economy of those *C. namaquensis* inhabiting regions outside the fog belt.

Chamaeleo pumilus adults were most dense in December (195 individuals, 2 437,5 g per hectare), with significant secondary peaks in January (118 individuals, 1 105,0 g per hectare), and October (120 individuals, 1 116,0 g per hectare). Juveniles were most dense in February and March as components of the overall population. Of all *C. pumilus* marked in February 1969, 40% were recovered two years later. Biomass and density of adult *C. namaquensis* were relatively consistent, increases in the biomass reflecting the heavier weights of gravid females. *C. namaquensis* also had a high recovery rate.

C. pumilus and *C. namaquensis* display in a series of side-to-side head bobs. *C. pumilus* and *C. namaquensis* resort to fighting if the transgressing chamaeleon does not leave the defender's presence.

Both sexes of *C. pumilus* have an undefended, shifting, vertical home range averaging 10 m^2 in plan view. However, since these chamaeleons use their home ranges as if they were layered, the actual area is about 600 m^2. If the food sources failed, the home range locus was shifted. Only a favoured perch was defended by both sexes of this species.

C. namaquensis occupied very rigidly delimited territories. Female territories and territories limited to one biotope or habitat were the smallest. Male territories increased in area during courting and those of females enlarged during egg-laying. Juveniles occupied a small, shifting home range within the rigidly defended territories of the adults from whom they were free of challenge.

In June and July male *C. pumilus* showed total regression of the testes and in August most male *C. namaquensis* had inactive testes. Yolk deposition occurred in follicles of 2 mm diameter in adult female *C. pumilus* and *C. namaquensis*. *C. pumilus* eggs were ovulated at 7,0–8,0 × 6,0–6,5 mm and in *C. namaquensis* at a diameter of 13 mm or greater. Development of ovarian follicles is brought to and held at 4 mm diameter if oviducal development of embryos or eggs is in progress. Ovarian follicular development does not proceed until the litter developing in *C. pumilus* had at least reached pholidosis and in *C. namaquensis* until the oviducal eggs were being shelled or their laying was imminent. Recently ovulated *C. namaquensis* eggs have a reddish embryonic area of 2 mm, and at the time of oviposition this area was as great as 10 mm.

The gestation period in *C. pumilus* was as short as 60 days in the case of litters conceived in March and born in May to as long as about 90 days at other times. Gestation lasted 35–45 days in *C. namaquensis*. *C. pumilus* females about to give birth select small-leaved shrubs, and *C. namaquensis* females oviposit in burrows which they dig to a depth of 200–250 mm.

Sexually mature female *Chamaeleo pumilus* had four litters annually, the size of the female having some relation to the size of the litter. Births were recorded in February to May, September, November and December. The largest litters (5–21; $\bar{x} = 17,0$ young) were born in December; the smallest in April (3–6; $\bar{x} = 4,5$ young), for an overall range of 3–21 ($\bar{x} = 11,0$ young). Newly born *C. pumilus* quickly freed themselves of their membranes, and have a mean snout-vent of about 22 mm; the smallest are those born in September (snout-vent mean of 20 mm) and the largest those born in November (snout-vent mean of 25 mm). The pattern of the young differs from that of the adults.

Growth is rapid, maturity being reached in both sexes at a snout-vent of 50 mm, taking 85 days for those born in November to as much as 240 days in those born in March, April and May.

C. namaquensis had at least two to three clutches of eggs per year, and these eggs are laid from May to September. Clutches laid in September (6–13; $\bar{x} = 9{,}5$ eggs) were the smallest in complement and those laid in July (10–22; $\bar{x} = 13{,}0$ eggs) were the largest. Of 250 *C. namaquensis* eggs examined, sizes at oviposition varied from $17{,}5–26{,}0 \times 10{,}0–14{,}5$ mm; 1,2–2,8 g ($\bar{x} = 20{,}5 \times 11{,}6$ mm; 1,5 g). Eggs laid in September were slightly larger than those laid at other times. When first laid, eggs were beige, becoming immaculate white with thin parchment-like shells.

Eggs laid in early August, September, and October took 91 days to hatch, while those laid in May took 112 days. The overall incubation period was 98,4 days. The length of the incubation period is apparently related to the temperatures at the depth at which the eggs were laid. The overall incubation increment of *C. namaquensis* eggs was: length 14–40% ($\bar{x} = 19{,}8\%$); width 4–16% ($\bar{x} = 9{,}8\%$); and weight 18–65% ($\bar{x} = 37{,}0\%$).

Recently hatched male *C. namaquensis* varied in total length from 45–55 mm and all weighed about 0,6 g. Females were larger, varying in total length from 55–65 mm and weighed 1,0–1,7 g ($\bar{x} = 1{,}5$ g). They were identical to the adults in appearance, except the young had more vertebral knobs. The young have an affinity for climbing. Male *C. namaquensis* matured in 210 days at a snout-vent of 70–75 mm and females in 150 days at a snout-vent of 75–80 mm.

Excision of the fat bodies resulted in a decline of testicular activity in four males each of *C. pumilus* and *C. namaquensis*. Excision of the fat bodies in four female *C. namaquensis* retarded or prevented ovarian follicular growth in pre-estrous females. In early estrous females fat body excision induced a high incidence of follicular atresia and retarded the yolk deposition rate. In six female *Chamaeleo pumilus* fat body excision retarded or prevented ovarian follicular development, and only pregnant females with the young near birth actually completed delivery.

Corpora lutea were large and prominent in *C. pumilus* and *C. namaquensis* females during the gestation period. Excision of corpora lutea in five pregnant female *C. pumilus* had no effect on litter development of those young that had passed pholidosis, but in those females with more immature young, corpora lutea excision resulted in resorbtion. In four gravid female *C. namaquensis*, excision of the corpora lutea did not affect the oviposition of those eggs about to be laid, but recently ovulated eggs were resorbed. Developing oviducal embryos in *C. pumilus* and developing oviducal eggs in *C. namaquensis* apparently rest in specific chambers in the oviducts during gestation, and if insufficient sites are available in *C. pumilus*, the surplus ovulated eggs were resorbed and their corpora lutea degenerated.

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